AN

INTRODUCTION

TO

NEMATOLOGY

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1881—1938

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PREFACE

I wish to express my appreciation to Doctor G. Steiner, Doctor J. R. Christie and Miss E. M. Buhrer, of the Division of Nematology, U. S. Bureau of Plant Industry, for their helpful suggestions concerning certain subjects and criticisms of the chapters I have written wholly or in part. To Dr. H. J. Van Cleave of the Department of Zoology, University of Illinois, gratitude is due for his criticisms of the chapter on "Nemic Relationships"; as was to be expected he did not wholly agree with the treatment of this controversial subject. Mr. Jonas Bassen of the U. S. Bureau of Entomology and Plant Quarantine has aided through the translation of Russian articles and Miss Dorothy Bero has checked the bibliographies.

Mr. G. A. Grille of the Spencer Lens Company, Washington, D. C., kindly supplied the photograph of Dr. Hall.

Section I, Part III includes a chapter by Doctor Reed O. Christenson with contributions by Dr. F. G. Wallace, Mr. Leon Jacobs and Mrs. M. B. Chitwood. Section II, Part I contains chapters by Dr. A. C. Walton and Mrs. M. B. Chitwood; they assume full responsibility for the contents of their chapters unless otherwise noted. I wish to express my appreciation for the fine way I feel they have handled their subjects. I assume responsibility for the nomenclature used.

B. G. C.

CHAPTER IX.

THE EXCRETORY SYSTEM

M. B. CHITWOOD and B. G. CHITWOOD

Introduction

The structures which at present are termed "excretory" system have been the subject of many arguments into which little evidence has been introduced. An excretory function has not always been presumed for these structures and in some instances other structures have been termed excretory organs.

Bojanus (1817), studying *Parascaris equorum*, discovered a pair of lateral vessels contained within the lateral chords and anastomosing in a bridge beyond which they continued. Later (1821) the same author thought he saw a row of lateral stigmata in *Rhaphidascaris acus* and he finally concluded that the lateral canals were blood vessels and the "büschelförmigen Organe" with which they are sometimes associated were gills.

Cloquet (1824) likewise observed lateral vessels and their anastomosis anteriorly; it was his opinion also that the vessels were circulatory. Mehlis (1831) observed a gland opening near the head in *Contracaecum spiculigerum* and paired strand-like bodies (glands) in strongylids opening at the mouth. He presumed both to be salivary glands, but Schneider later interpreted these structures as excretory glands in both cases.

Shortly thereafter von Siebold in an appendix to a thesis by Bagge (1841) noted the existence of a ventral pore connected with paired lateral canals in *Oswaldocruzia* (*Strongyles auricularis*) and *Aplectana*. (*Ascaris acuminata*) but he did not, at that time, express any view to the function of these structures.

Blanchard (1847) injected specimens of *Ascaris lumbricoides* and upon seeing a large ovoid body in the left lateral chord (the gland nucleus, Fig. 112H) he decided that he had found the heart and he also maintained that there is a second pair of vessels just under the cuticle. On this basis he decided this system to be circulatory.

Leidy (1853) observed a "follicle communicating with the exterior and having its bottom connected by means of radiating bands to the external surface of the alimentary canal" in *Thelastoma attenuatum* and *Aorurus agile*. He was followed by Huxley (1856) and Wagener (1857) who recognized the full extent of the lateral vessels in *Oswaldocruzia filiformis* (*Strongylus auricularis*) and *Heterakis* sp., respectively. It was at this time that Davaine (1857) described a ventral tube and a lateral vessel (on one side only) in *Anguina tritici*.

Schneider (1858, 1860, 1863, 1866) was the first worker to draw the various isolated bits of information together, synthesize, examine critically and summarize. He first proved Blanchard's concept regarding *Ascaris lumbricoides* to be erroneous, showing that what was interpreted as the heart is a large nucleus in the vessel wall, that there is only one pair of vessels and they unite to open through the ventral pore. He likewise established the fact that the ventral pore and canals are joined in the oxyuroids and strongylins; he saw the labyrinthoid coils of the posterior termination of the vessels in *Alloionema appendiculatum*; and also observed the two strand-like bodies ("Subventral" or "cervical" glands) that are attached to the anastomosis or bridge in *Rhabditis strongyloides* and *Strongylus* spp. He further expressed the view that lateral vessels are present in all "mero" and "polymyarian" nemas and usually absent in "holomyarian" nemas (except *Anguina tritici*); and finally he (1866, p. 220) concluded that this system of vessels must be related to the excretion of chemical waste products as in the excretory system of all other worms.

Meanwhile Eberth (1860, 1863) erroneously described paired lateral vessels in *Heterakis gallinae*, with two anterior and two posterior lateral openings (amphids and phasmids respectively) and in *Passalurus* he apparently did not differentiate between vessel and chord. In reference to marine nematodes he was more accurate in describing a fine pore near the head and a clear tube proceeding posteriorly in the esophageal region of *Oncholaimus*, *Enchelidium*, and *Enoplus*.

Bastian (1866) verified many of Schneider's observations, proved the general existence of a "ventral" gland in marine and fresh water nemas and definitely showed that the "water vascular system" (vessels) in parasitic nemas and the ventral gland in free-living forms "are only modifications of one and the same structure." While drawing attention to a similar system in trematodes he noted that in no instance have vibratile cilia been observed in the canals of nematodes and that in neither nematodes nor trematodes is the system adapted to respiratory activity. He concluded that it must be excretory.

General Morphology. The diversity of the nemic excretory system makes it a difficult system to interpret. The general concept of a unicellular system probably originated with Bastian's homologizing of the single ventral gland of marine nemas with the tubular system. Though neither Bastian nor Schneider emphasizes the point, only one nucleus (the sinus nucleus) was known in *Ascaris;* nevertheless they knew of two cells associated with the sinus in rhabditids and strongylins (Fig. 112 I-L). Cobb's description (1890) of the origin of the excretory system in the first stage larva of *Enterobius vermicularis* as an outgrowth of a single invaginated hypodermal cell has given much impetus to the primary single cell concept. Later (1925) the same author described the system in mature embryos of *Rhabditis icosiensis* as consisting of a single gland cell, terminal duct, and paired lateral canals in a ventral position, i. e., not in the lateral chords; according to his view the paired subventral glands are derived from the single cell by splitting and the canals are merely outgrowths. Study of the excretory system in young specimens is technically very difficult and open to considerable error due to the delicacy of the structures. As indicated by Cobb's own figures and verified in diverse instances by the writers the system in first stage larvae is much nearer to that of the adult than is commonly supposed. Actually, we have been unable to establish with certainty any difference between larva and adult. In our opinion the common pore and cell illustration in larval nematodes represents only the obvious features. The fact that neither Cobb nor other adherants of the unicellular gland idea have accounted for or even recognized the existence of a terminal duct cell in addition to glands or sinus cells makes us most dubious of the entire concept.

The second concept of the system is based upon its identity with the protonephridial system of trematodes, rotifers, gastrotrichs, etc. This viewpoint was accepted by Bastian (1866) and Schneider (1866) without particular question. It likewise seemed reasonable to Bütschli (1876) and Martini (1916). It has fallen into disfavor recently because it cannot be accepted by those presuming the marine aphasmidian (having a single ventral gland cell) as primitive. These authors (Filipjev, Stekhoven) must assume the system to arise de novo in the Nematoda or assume that the remainder of the Animal Kingdom arose from nematodes. They have apparently chosen the first alternative though with odd consistency at the same time relating nematodes, rotifers, echinoderes, gastrotrichs and nematomorphs. Steiner (1919, 1920) brought out a series of diagrams hypothetically indicating the mode of evolution of the nemic excretory system from that of the rotifer. His diagrams give interesting points but overlook the essential complexity of the tubular system of both groups. We shall not go into such matters at the present. The most necessary evidence, critical embryological study, is lacking.

Golowin (1902) expressed the view that the tubular, cuticularly lined terminal duct cell is an invagination of the hypodermis which meets and fuses with the lateral canals and excretory sinus. This view was concurred in by Goldschmidt (1906) and has rather significant support. It accounts for the collecting tubes as a separate entity, not developed from a ventral gland; these tubes may be considered as derivatives of the basic protonephridial system without reorientation of the system; it accounts for the minimum two to three cell

system in the Phasmidia as well as the ventral gland of marine forms without assuming either de-differentiation of the protonephridial system or de novo formation within the Nematoda. Properly speaking, the various nemic excretory systems have only one point in common, namely that they open through a ventral pore.

Von Linstow (1909) presented a classification of the Nematoda, based on the excretory system, which has considerable merit though it is in disrepute because the original author incorrectly placed many forms. The general outline may be summarized as follows

I. Secernentes. Lateral canals emptying anteriorly through a ventral pore; chords narrow and high. [*Ascaris, Oxyuris, Oxysoma, Nematoxys, Heterakis, Strongylus, Cucullanus, Dacnitis, Spiroxys, Rictularia, Cheiracanthus* (*Gnathostoma*), *Tropidocerca, Ancyracanthus*].

II. Resorbentes. Lateral canals absent, excretory pore absent; chords 1/6 periphery; esophagus and gut often atrophied. Feeding by resorption through cuticle. [*Angiostoma* (*Rhabdias*), *Eustrongylus* (*Dioctophyma*), *Hedruris, Dispharagus, Ichthyonema* (*Philometra*), *Filaria*].

III. Pleuromyarii. Muscles extending over lateral lines; excretory system absent, male with one spicule. [*Hystrichus, Trichocephalus* (*Trichuris*), *Trichosoma* (*Trichosomoides*)].

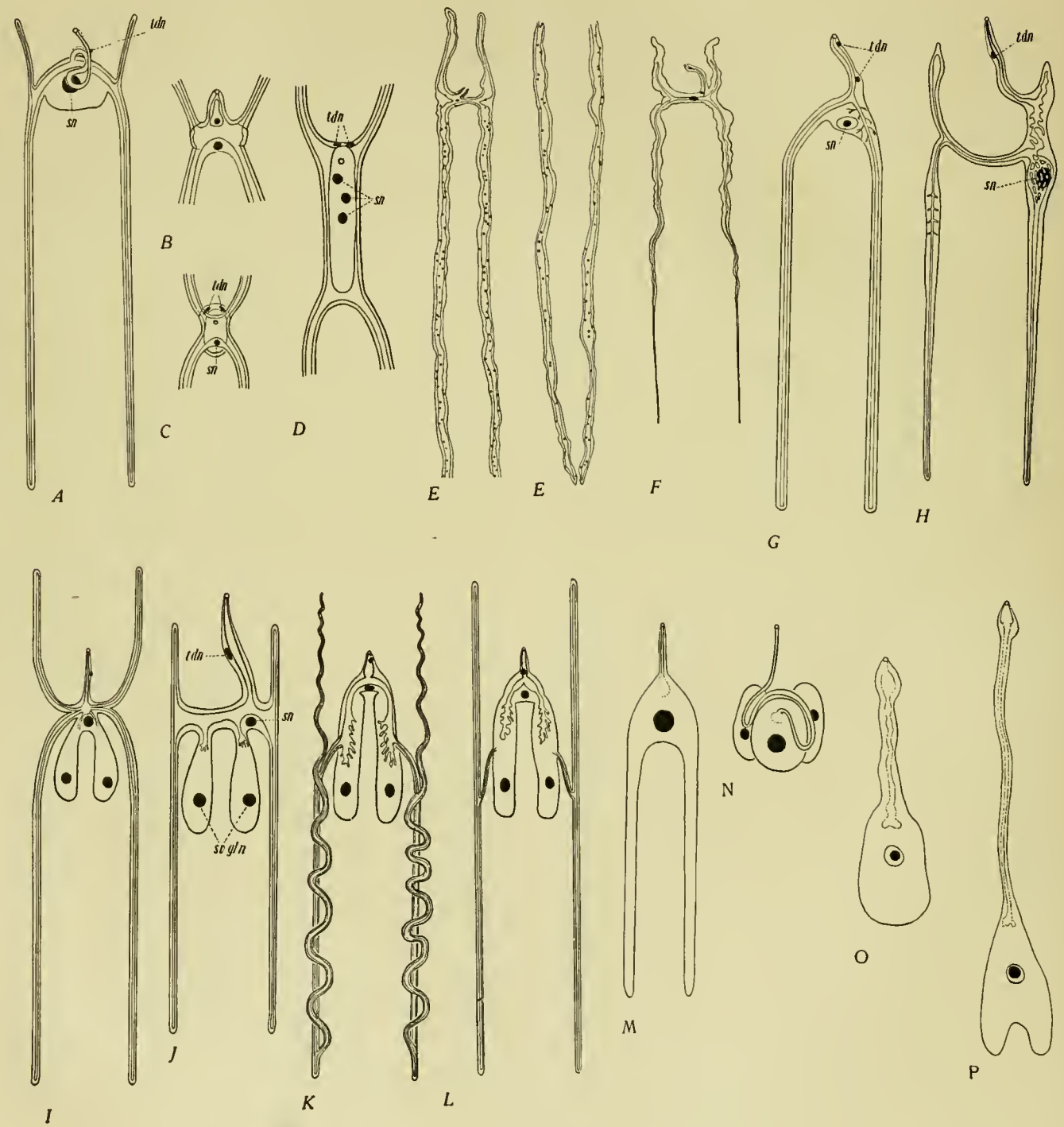

Fig. 112. DIAGRAMS OF NEMIC EXCRETORY SYSTEMS.

A—*Rhabditis dolichura;* B—*Heterakis gallinae;* C—*Macracis monhystera;* D—*Spironoura affine;* E—*Cucullanus heterochrous;* F—*Camallanus lacustris;* G—*Camallanus microcephalus;* H—*Ascoris lumbricoides;* I—*Rhabditis strongyloides;* J—*Metastrongylus elongatus;* K—*Strongylus equinus;* L—*Oesophagostomum dentatum;* M—*Anonchus mirabilis;* N—*Anaplectus granulosus;* O—*Chromadora quadrilinea;* P—*Phanodermopsis longisetae.* E & F, After Toernquist, 1931, Goeteborgs Kungl. Vetensk. Vitterhets—Samh. Handl. s. B., v. 2 (3): 1-441, figs. 1-13, pls. 1-17. Remainder original.

IV. Adenophori. Small high lateral chords; ventral pore present, connected with a ventral cervical gland; two spicules; herein the free-living nematodes should be placed. (*Myenchus, Myoryctes, Rhabditis, Cephalobus*).

The Secernentes by definition correspond to the Phasmidia and the examples include representatives of four out of five of the major phasmidian groups, i. e., Strongylina, Ascaridina, Camallanina and Spirurina. The group Resorbentes was less fortunately constituted, since it was primarily based upon a supposed method of feeding which the author attempted to correlate with anatomy. On the basis of present day information all representatives except *Dioctophyma* would be placed in the Secernentes. The exceptional genus might be placed with the Pleuromyarii (on the basis of one spicule) or the Adenophori (on the basis of chords). From the standpoint of excretory system, or lack of it, the Pleuromyarii must be considered synonymous with the Adenophori. Steiner (1919) criticised von Linstow rather severely for having put forward such a classification because it was well known that *Rhabditis* and *Cephalobus* had lateral excretory canals. The evidence today shows that Linstow was in error as to all of the examples of the Adenophori which he listed. However, it should be recognized that Linstow was right in his fundamental conception. Most free-living nemas differ from typical parasitic nemas in that they have no lateral excretory canals. Linstow had little choice of example since he was discussing the parasitic nemas and covered free-living forms only to the extent that they occurred as parasites.

Today we find ourselves following very closely the definitions Secernentes and Adenophori as given by von Linstow though ignoring his examples. The Secernentes are absolutely equivalent to the Phasmidia while the Adenophori correspond to the Aphasmidia. It is of further interest to note that the presence of lateral canals is always evidenced by a cuticularly lined terminal duct or excretory vesicle; furthermore, the reverse is also true with only two exceptional instances (Plectidae and larval mermithids). In all instances carefully investigated in recent years, the tubular excretory system occurring in the Phasmidia has been found to consist of not less than two cells, one or more forming the cuticularly lined terminal duct and one or more forming the lateral canals and glandular tissue. The Aphasmidian unicellular gland lacks the cuticular lining of the terminal duct and consists of a single gland cell with no canals. We may conceive of this system as the homologue not of the entire Phasmidian system but only of the ectodermal part, i. e., the terminal duct cell.

Secernentes (Phasmidia)

In the first group, there are four chief modifications of the excretory system (Fig. 9, p. 11), namely (1) the oxyuroid or simple H system (oxyuroids, some ascaridoids, some scattered members of the Spirurina); (2) the rhabditoid system, a combination of the H type with two subventral glands (known in some rhabditids and strongylins); (3) the ascaridid inverted U-system, characteristic of ascaridids but occurring also in most members of the Spirurina and some free-living forms (*Panagrolaimus*); (4) the asymmetric system, known only in Anisakinae and Tylenchoidea.

Critical study indicates types (3) and (4) have appeared more than once in the general evolution and both types may be considered as ordinary variations of type (1). Type (2) is known only in one parasitic group, the Strongylina and in some representatives of one free-living group, the Rhabditidae.. Normal progressive evolution would account for the origin of the rhabditoid system from the oxyuroid system.

(1) Simple H System. This type, commonly spoken of as the oxyuroid system, is by no means limited to oxyuroids. There are several variants of the system, chiefly dependent upon the form of the terminal excretory duct.

(a) Terminal duct long and tubular.
(b) Terminal duct greatly shortened, but not vesicle-like.
(c) Terminal duct elongate, vesiculate.
(d) Terminal duct a very short vesicle.

(1a) Presumably, the elongate, cuticularly lined terminal duct is the more primitive type. In such a system one finds at least one, sometimes two nuclei attached to the terminal duct and one large sinus nucleus. Long anterior canals are known only in free-living nemas such as *Rhabditis dolichura* and *Cheilobus schneideri* (Fig. 112A). Excretory systems of such forms have been studied by Bütschli (1873), Jägerskiöld (1909), Magath (1919) and Törnquist (1931). Undoubtedly this type of system is more widespread in the Rhabditoidea than is known; it is very closely approached in ascaridids. Törnquist found representatives of both the Camallanidae and Cucullanidae with H type systems and both H and inverted U forms existing within the two genera *Procamallanus* and *Camallanus*, the H type being confined to camallanids of fish. There are really two quite distinct forms for this system. In *Camallanus* (Fig. 112 F-G) one finds two nuclei within the wall of the terminal duct, one nucleus near the pore and one near the anterior surface of the sinus. In this case the terminal duct connects with the sinus near the left lateral chord and there is a large sinus nucleus on the left side (Fig. 114 CC). The lateral canals begin as thick walled tubes, sometimes with indistinct, questionable, tributary tubules; thereafter the canals become smaller and they never have a thick lining nor have nuclei been observed in their walls. This, then, is a three nucleate or three celled system.

In *Cucullanus*, according to Törnquist, (1931) sometimes the terminal duct is dilated like a bladder near the pore (like b or d). There is no distinctive sinus nucleus but there are many similar nuclei within the walls of the posterior lateral canals which should probably be interpreted as multiples of the original sinus nucleus (Fig. 112 E). The walls of the lateral canals are thick throughout their length but are particularly massive in the cervical region and taper posteriad (Fig. 114 L). Distinct branching tubules penetrate the wall of each canal, these being best developed in the cervical region (Fig. 114 M); the tubules do not leave the canal tissue. Törnquist found such tubules arising more or less symmetrically in fours, two dorsolaterally and two ventrolaterally from the canal axis, while the writers have found six series of tubules more common, there being two lateral ones in addition to those previously mentioned.

The multinucleate character of the cucullanid excretory system was first noted by Jägerskiöld who considered the whole system as representing a polynucleate cell. Törnquist and the writers have confirmed Jägerskiöld in not being able to find cell walls. However, we may well question our interpretation of this case until further information is obtained relative to the occurrence of nuclei in lateral canals. Such findings are becoming common.

(1b) The shortened terminal duct type, as exemplified by *Heterakis gallinae* (Fig. 112 B), is very similar to (1a) and probably should be considered a modification thereof. The observations of Wagener (1857), Eberth (1860) and Schneider (1860) have previously been mentioned. More recently Chitwood (1931) and Baker (1936) have restudied this form. The excretory orifice is guarded anteriorly by a lip cell (Fig. 113 RR) formed from the anterior side of the terminal duct. Thence internally the terminal duct is wide, irregular until it merges with the excretory sinus. On the lower left hand side a small nucleus is present in the terminal duct wall (Fig. 113 JJ). The only means of distinguishing sinus and duct is through the cuticular lining of the duct. There is another nucleus on the ventral side associated with the sinus and terminal duct but apparently exterior to their walls (Fig. 113 KK); one often sees fibrous tissue around the duct and near this nucleus, and it seems possible that the nucleus and fibers represent a sphincter muscle of the sinus and terminal duct. The sinus nucleus itself is situated medially and is not especially large in *Heterakis* (Fig. 113 LL). No additional nuclei have been observed in the lateral canals. The heterakid system, therefore, seems to consist of not less than three nuclei or cells, two belonging to the duct and one to the sinus and canal system.

(1c) The elongate, vesicular terminal duct is another modification of type 1a; it is confined, so far as known, to the Kathlaniidae occurring in such forms as *Spironoura affine* and *Cissophylus roseus*. Whether or not it is a character of the entire family is not known. As Mackin (1936) observed, the anterior and posterior canals unite with their mates and empty into a great elongate sinus which separates anterior and posterior canals (Fig. 112 D). This is distinctly different from other forms in which the two anterior and two posterior canals all come together at practically the same level. Apparently this sinus combines the functions of terminal duct and sinus since there is a delicate cuticular ventral lining connected with the excretory pore; thus we might say the dorsal side is sinus and the ventral side is terminal duct. The excretory pore is at the anterior end of the excretory region (Fig. 113 NN) and near this region two small subventral nuclei are present; these we attribute to the terminal duct. The dorsal side of the sinus contains three equal, rather large nuclei (Fig. 113 MM). The tissue in which they are situated is continuous wi h the tissue of the lateral canals and in the latter no nuclei have been observed. On the basis of present information the *Spironoura* system contains five nuclei, three belonging to the canal system (sinus) and two to the duct.

(1d) The typical oxyurid excretory system is a notable feature in most representatives of the Oxyuridae, Thelastomatidae, and Atractidae. Due to the clarity of the oxyurid body and to the rather large diameter of the lateral canals, this form has become synonymous in the literature with the H system even though it is but one variant.

Leidy (1853), Eberth (1863), Schneider (1866), Bütschli (1871), Cobb (1890), Martini (1916), Rauther (1918), Thapar (1925), Chitwood (1931) and Chitwood and Chitwood (1933) have studied the system as seen in *Thelastoma, Passalurus, Oxyuris* (sensu lato), *Leidynema* and *Hammerschmidtiella, Enterobius vermicularis, Oxyuris equi, Macracis monhystera* and *Thelandros alatus*, various reptilian oxyurids (Pharyngodoninae), *Hystrignathus* and *Macracis*, and *Cephalobellus* respectively. Subsequently extension of observations has shown the system to be practically universal in the families mentioned. The four lateral canals come together at about the same level forming, with the sinus, an X (Fig. 112 C). The sinus nucleus may be medial as in *Hystrignathus* and *Macracis* or on the left side as in *Cephalobellus;* it is not proportionately very large. Chitwood (1931) described regularly arranged nuclei in the lateral canals of *Macracis monhystera* (Fig. 113 FF-GG). In other forms no such nuclei appear to be present. Constancy and recognition of the sinus nucleus in *Macracis* argue against the concept that the canal nuclei are derivatives of the sinus nucleus.

The excretory vesicle, bladder or reservoir is a most interesting structure showing considerable variety in oxyuroids. As in types 1b and 1c the terminal duct is in open connection with the excretory sinus (Fig. 113 V, *Cephalobellus*), its cuticular lining forming the ventral part of the sinus wall. As observed by Rauther (1918) in *Macracis*, the terminal duct wall contains two nuclei or is composed of two cells, these cells may both be situated anterior to the excretory pore or one may be anterior and one posterior. The conspicuous rounded vesicle seen in totomounts is apparently not a storage structure (see figs. 113 BB-CC) but more on the order of a valve; i. e., the sinus cavity functions as the reservoir while the terminal duct is shortened. Sometimes (Fig. 113 Y-Z) there is a distinct circular sphincter muscle near the junction of sinus and duct. In representatives of the Atractidae the wall of the terminal duct is radially striated from the excretory pore giving the appearance of a sucker.

Martini (1916) saw structures which he considered might be rudimentary cilia near the blind ends of the excretory canals of *Oxyuris equi*. The writers have not observed such structures in the species studied.

(2) The Rhabditoid System (Fig. 112 I). The essential features of this system include (a) a terminal elongate cuticular duct, (b) an excretory sinus connected with paired lateral canals, and (c) paired subventral excretory glands also connected with the excretory sinus.

Mehlis (1831) supposedly observed the subventral glands (strand-like organs) in strongyles and thought they opened anteriorly as salivary glands. He may have confused the subventral excretory glands (cervical glands of Looss) with the amphidial glands (cephalic glands of Looss, fig. 12 G-I). In 1841 von Siebold observed the pore and vessels in *Oswaldocruzia* (*Strongylus auricularis*) and shortly thereafter Dubini (1843) associated the subventral glands of *Ancylostoma duodenale* with the esophagus and Bilharz (1852) observed the junction of subventral glands and excretory pore but did not see the lateral vessels. It was Schneider (1858-1866) who first observed the full gross morphology of the system by noting all three of the essential components (see above) and by joining them. However, he erred in one respect, by considering the gland cells as non-glandular attachments of the sinus (or bridge). Schneider's observations were made in reference to *Rhabditis strongyloides* (Fig. 112 I), *Cylicostomum tetracanthum, Strongylus armatus* and other strongyloids. Bütschli (1873) found *Rhabditis terricola* to have the same type of excretory system as that described by Schneider for *R. strongyloides*. Leuckart (1876) did the same in regard to *Ancylostoma duodenale*. Since that time papers dealing with the excretory system as seen in rhabditids and strongylins have been published by Rzewuski (1887), *Metastrongylus elongatus;* Stadelmann (1891), *Ostertagia ostertagi;* Augstein (1894), *Dictyocaulus filaria*; Looss (1895), *Trichostrongylus colubriformis;* Poeppel (1897), *Strongylus vulgaris;* Looss (1905), *Ancylostoma duodenale*; Maupas (1916), *Rhabdias* spp.; Cobb (1925), *R. icosiensis*; Aubertot (1926), *R. pellio*; Stekhoven (1926), *Ancylostoma* and *Necator;* Chitwood (1930, 1931), Rhabditis spp., and *Oesophagostomum dentatum;* Eisma (1932), *Ancylostoma*; and Raven and Stekhoven, (1934), *Rhabditis* spp.*

*As already noted, the "rhabditoid" excretory system does not occur in all rhabditoids, but is merely characteristic of a limited group centered around *Rhabditis strongyloides*. The majority of rhabditoids, including *Rhabditis dolichura* and other *Rhabditis sensu lato* have an H-shaped (oxyuroid) system. Raven and Stekhoven (1934) denied the existence of lateral canals in *Rhabditella oxei*, but the writers have re-examined this species and can confirm the previous observation of Chitwood (1930) that the system in this form is of the "rhabditoid" type—an H system with distinct sinus nucleus and two subventral glands

Fig. 113.

A—*Rhabditis sergenti* (Female with both ordinary and auxiliary excretory systems shown in outline); C—*Rhabditis seurati* (Female excretory systems shown in outline); B, D, & E—*Rhabditis icosiensis* (B—Posterior part of female showing auxiliary excretory system; D—Terminal duct of auxiliary system; E—Blind end of auxiliary system, all drawings semi-diagrammatic); F—*Rhabditis coarctata* (Auxiliary canal, regions drawn camera lucida from living specimen; the large nucleus could not be seen in the canal on the opposite side and it may not actually be within the duct wall); G—*Rhabditis terricola* (Blind end of auxiliary canal as seen in living specimen); H—*Ditylenchus dipsaci* (Cross section showing sinus nucleus in lateral chord); I-P—*Oesophagostomum dentatum*, cross sections (I—Near base of esophagus showing subventral glands, lateral canals, and amphidial glands; J—Subventral gland at level of nucleus; K—Terminal duct at excretory pore; L—Sinus with its nucleus; M-O—Approach and fusion of lateral and transverse canals; P—Lateral chord with lateral canal in mid-region of body); Q—*Metastrongylus elongatus* (Cross section at level of sinus, with its nucleus and connection with subventral glands); R-S—*Strongylus equinus* (R—Cross section of lateral chord in posterior region of female showing two lateral canals, one in cross section, the other longitudinal; S—Cross section of lateral canals about to fuse in preanal region of male; note round body which stained like a nucleus); T—*Rictularia coloradiensis* (Terminal duct at level of nucleus); U-V—*Cephalobellus papilliger* (U—Excretory sinus; V—sagittal section through terminal duct); W-AA—*Hystrignathus rigidus* (W-Z—Serial sections through terminal duct and sinus; AA—Cross section of another specimen at same level as that shown in W); BB-GG—*Macracis monhystera* (BB—Longitudinal section through terminal duct; CC—Cross section through excretory sinus; DD—Cross section of entire specimen at level of CC; FF—Lateral canal in chord showing nucleus in its wall; GG—Same as FF, seen in longitudinal section); HH—*Cucullanus serratus* (Lateral canal showing bacillary layer or possible cilia); II-LL & RR—*Heterakis gallinae* (II—Terminal duct; JJ—Second terminal duct nucleus, at level of sinus; KK—Sinus with possible constrictor nucleus; LL—Sinus nucleus; RR—Terminal duct with first terminal duct nucleus); MM-NN—*Spironoura affine* (MM—Cross section at level of first sinus nucleus; NN—Sagittal section through sinus); OO-PP—*Goezia annulatus* (OO—Entire excretory system; PP—Blind end of system); QQ—*Panagrolaimus subelongatus* (Blind end of lateral canal). A-E, After Maupas, 1916. Compt. Rend. Soc. Biol. v. 79: I-J. After Chitwood, 1931, Ztschr. Morph. v. 23 (½); U-V, After Chitw. & Chitw., 1933, Ztschr. Zellforsch. v. 19 (2); HH—After Toernquist, 1931, Goeteborgs Kungl. Vetensk. o. Vitterhets. Handl. s. B., v. 2 (3); OO-PP, After Hamann, 1895, Die Nemathelminthen v. 2. Remainder original.

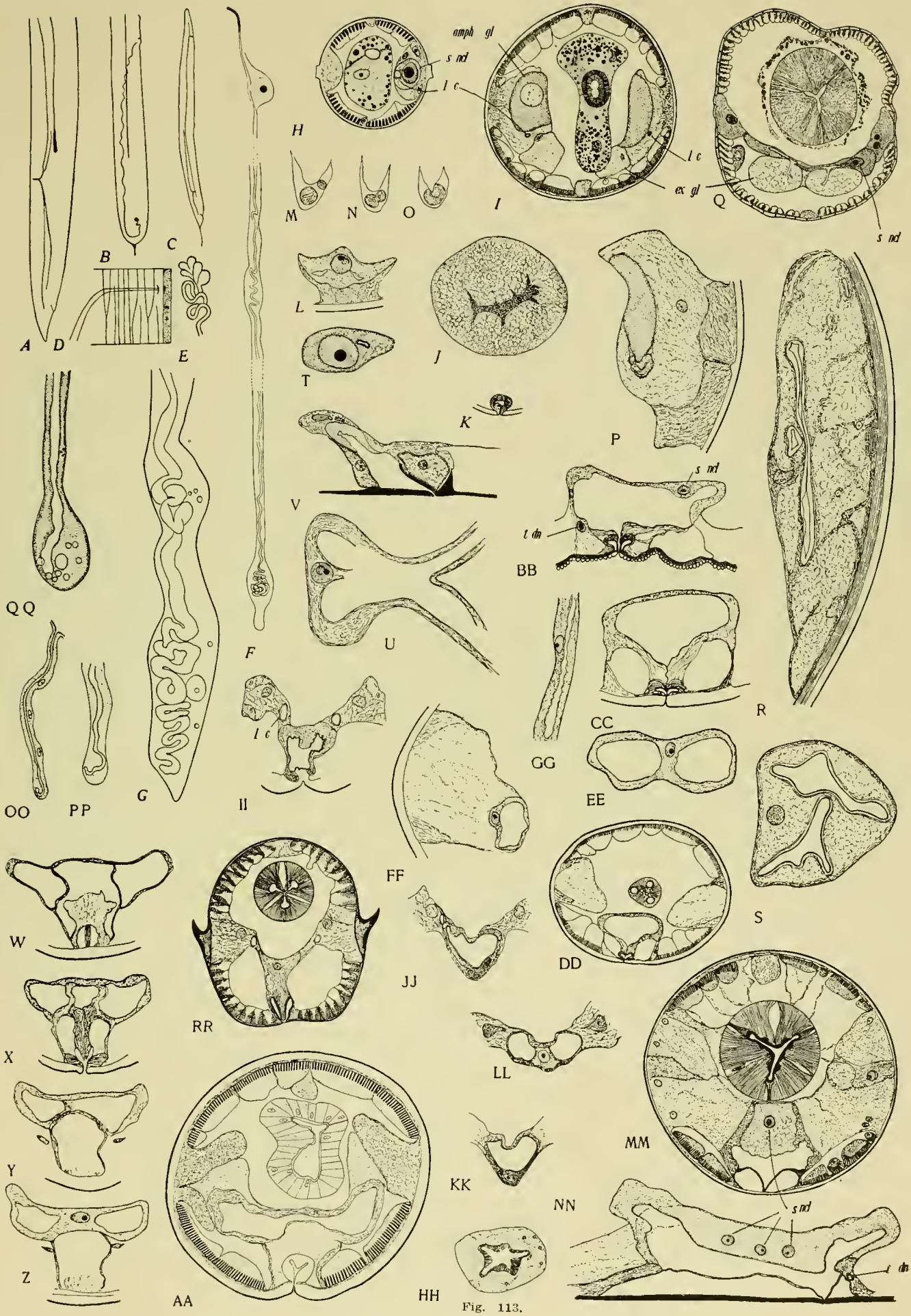
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Fig. 113.

According to our observations this system consists of not less than three, usually four cells in such diverse forms as *Rhabditis strongyloides*, *Oesophagostomum dentatum*, *Kalicephalus* sp. and *Metastrongylus elongatus*. The terminal duct is narrow, elongate and tubular in adult rhabditids as well as larval strongylins while it becomes folded and thick-walled (Fig. 113 K) in adult strongylins. Its nucleus lies just posterior to the end of the cuticular lining in these forms and corresponds to the carrying cell of the excretory vesicle described by Looss (1905) in *Ancylostoma*. It has been clearly identified in *Oesophagostomum*, *Metastrongylus* and *Strongylus*. More posteriad, the excretory canal widens into the transverse excretory sinus into which the paired subventral glands open. The excretory sinus contains a large conspicuous nucleus (Fig. 113 L) which may be medial (*Rhabditis strongyloides*, *R. coarctata*, *Oesophagostomum*) or left (*Metastrongylus*) in position. Thin-walled branching tubules extend posteriorly from the sinus into each of the subventral glands. The lateral canals may connect directly with the excretory sinus as in *Rhabditis* and *Metastrongylus* or they may connect indirectly by way of the subventral gland cells as in *Oesophagostomum*, *Ancylostoma* (vide Looss) and *Strongylus* (vide Schneider's description of double lateral canals). In the latter instance one finds two pairs of lateral canals in each chord extending nearly to the caudal extremity before they unite (Fig. 113 R). In other forms the lateral canals are tubular, delicate and usually extend nearly to the two extremities; often vacuoles may be seen in the wall of living specimens; each canal ends blindly at its terminus, often in a small ampulla. Thus far no one has identified nuclei in the lateral canals but this may be due to lack of critical study. In a complete series of cross sections of a male *Strongylus* the writers observed only one possible canal nucleus (Fig. 113 S) which was situated very close to the junction of the canals posteriorly; since it could not be verified in the corresponding canal in the other chord nor in other series, it may easily have been an artifact. Ordinarily the lateral canals in nemas are considered "outgrowths" of the cell which we have herein called the *sinus cell*. In the organization of *Oesophagostomum* and *Strongylus* such a relationship is seemingly precluded since the canals do not empty into the sinus directly, but through the subventral glands. One may conceive the *Rhabditis strongyloides* type (Fig. 112 I) to be most primitive, and transformation to the *Strongylus* type to have taken place by a posterior shifting of the canal union. In *Rhabditis* and *Strongylus* the sinus nucleus *plus the subventral gland nuclei* are therefore to be considered homologous to the sinus nucleus of oxyuroids and *Rhabditis dolichura*.

Maupas (1900) apparently first noted contraction in the lateral canals of *Rhabditis lucianii* and in 1916 the same author noted a contractile ampulla at the end of the terminal excretory duct in *R. terricola*. Similar observations were made concerning larvae of *R. pellio* by Aubertot (1926) and *Rhabditella axei* by Raven and Stekhoven (1934). The latter authors observed only one gland cell and presumed there would be two ampullae if there were that many gland cells. This is not necessarily the case. The ampulla corresponds apparently to the excretory sinus and may act as a central contractile bladder in which the various contents empty.

Plurality of lateral canals in the lateral chords has been recorded by Schneider (1866), Leuckart (1876), Poeppel (1897) and Looss (1902), the cases referring to strongyloids. Ultimately these canals have always been found to join and not to represent a real duplication or branching of the canals. However, in females of some species of rhabditids this is not the case. As first noted by Maupas (1916) there may be an auxiliary excretory system with paired openings dorso- or ventrolaterally posterior to the vulva. Maupas recorded such a system in *R. terricola*, *R. lucianii*, *R. axei*, *R. pellio*, *R. seurati*, *R. sergenti* and *Angiostoma limacis*. It was many years before the writers had the pleasure of seeing this system, and then only in *Rhabditis terricola*, *R. coarctata*, *R. cylindrica*, *Rhabditella axei* and *Rhabditoides paraelongata*. It does not seem to be present in *R. strongyloides*. Whether it may occur abnormally in that species or whether Maupas misidentified his species, we cannot say. The system as seen by us in *R. terricola* consists of two tubes, one in each lateral chord, connected by a ventrolateral pore near the vulva. The canals extend posteriorly to the caudal region, and are much coiled at the blind end (Fig. 113 F-G.) In *R. coarctata* a large nucleus seems to be associated with the terminal duct of the auxiliary system but it is not certain that the nucleus is in the duct wall. In *R. sergenti* Maupas found both an anterior and a posterior branch, each bifurcate (Fig. 113 A).

3. The ascaridid or inverted U-type. Historically one of the systems most commonly studied and referred to, it is not confined to ascaridids but occurs in spiruroids and in at least one group of rhabditoids (Cephalobidae). As pointed out by Törnquist (1931) polyphyletic origin of the inverted U type from the H form occurs even within genera and this system cannot be regarded as separate and distinct from 1a. The essential parts are an elongate, cuticularly lined terminal duct, a sinus, and two posterior lateral canals. By custom *Ascaris lumbricoides* is retained in this classification though distinct rudiments of anterior canals are present (Fig. 112 H).

The system as described in *Ascaris lumbricoides* and *Parascaris equorum* by Goldschmidt (1906) consists of three cells, one nucleus in the wall of the terminal duct, another in the protoplasmic part of the "anterior bridge" and a third, the giant excretory nucleus in the left lateral chord. Mueller (1929) by means of injections showed Goldschmidt in error relative to the existence of both an anterior and posterior "bridge" (sinus). As found by Mueller and verified in sections by the writer, the terminal duct leads to the left lateral canal with which it connects very close to the anterior extremity of the canal; the right lateral canal extends further anterior than the left, indeed nearly to the level of the excretory pore. The excretory sinus is quite variable, its lumen branching and anastomosing (Fig. 114 A-B & E). The writers found a single nucleus (Fig. 114 F) definitely within the wall of the terminal duct about half way along its length. The gigantic sinus nucleus of *Ascaris* is moved to the left lateral chord and is surrounded by branching capillaries of the left lateral canal. These branchings become less marked posteriorly and finally fuse forming a typically simple canal. The canal may give off minute tubules (Fig. 114 C) as were previously noted in *Cucullanus* but no additional nuclei have thus far been observed in the canal walls. Goldschmidt (1906) thought the tubules extended into the adjacent areas of the chords and they were the actual secreting part or glandular structure. Subsequent work has disproved this hypothesis.

The camallanid inverted U system is essentially the same as the H system found in that group and requires no especial comment. In filarioids, spiruroids and dracunculoids the inverted U system is apparent in totomounts used for taxonomic study (Fig. 14 I & L) but has not been subjected to critical analysis. The same is equally true of cephalobids such as *Panagrolaimus subelongatus*.

Fig. 114.

A-F—*Ascaris lumbricoides* (A—Analine blue-black injected specimen showing terminal duct, sinus and associated tubules; B—Details of same region showing sinus nucleus; C—Right lateral chord showing canal branches; D-E—Left lateral chord in sinus region, D—at level of sinus nucleus; E—anterior to that level; F—Terminal duct nucleus); G-J & O—*Anisakis simplex* (G—Detail of tubule branching and terminal acini; H-J—Cross sections through sinus cell at level of nucleus, H of a young specimen, I of an older specimen, O and J of a senescent specimen); K—*Loa loa* (Excretory pore and cell in microfilaria); L-M—*Cucullanus* sp. (L—Lateral chord and canal near sinus; M—same in posterior part of body); N—*Mermis brevis* (Lateral view of anterior end of adult, showing excretory cell); P-R—*Phanodermopsis longisetae* (P—Excretory pore and terminal ampulla; Q—Esophageal region; R—Cross section at level of excretory cell); S-U—*Enoplus communis* (S—Cross section at level of excretory nucleus; T—cross section posterior to S; U—Ventral view of excretory cell as seen in toto); V-W—*Anoplectus granulosus* (V—Cross section at level of ventral gland cell; W—Ventral view of excretory system and associated structures as seen in toto); X—*Chromadora quadrilinea* (Esophageal region); Y—*Spilophorella paradoxa* (Cross section at level of excretory cell); Z-CC—*Camallanus microcephalus* (Z—Terminal duct showing first nucleus; AA—Terminal duct showing second nucleus; BB—End of terminal duct connecting with sinus; CC—Sinus with its nucleus). A-B, After Mueller, 1929, Ztschr. Zellforsch. v. 8 (3); G-J & O, After Mueller, 1927, Ztschr. Zellforsch. v. 5 (4); K, After Fuelleborn, 1929, Handb. Path. Microorgan. v. 6 (2); N, After Hagmeier, 1912, Zool. Jahrb. v. 32 (6); U, After de Man, 1886, Nordsee Nematoden. Remainder original.

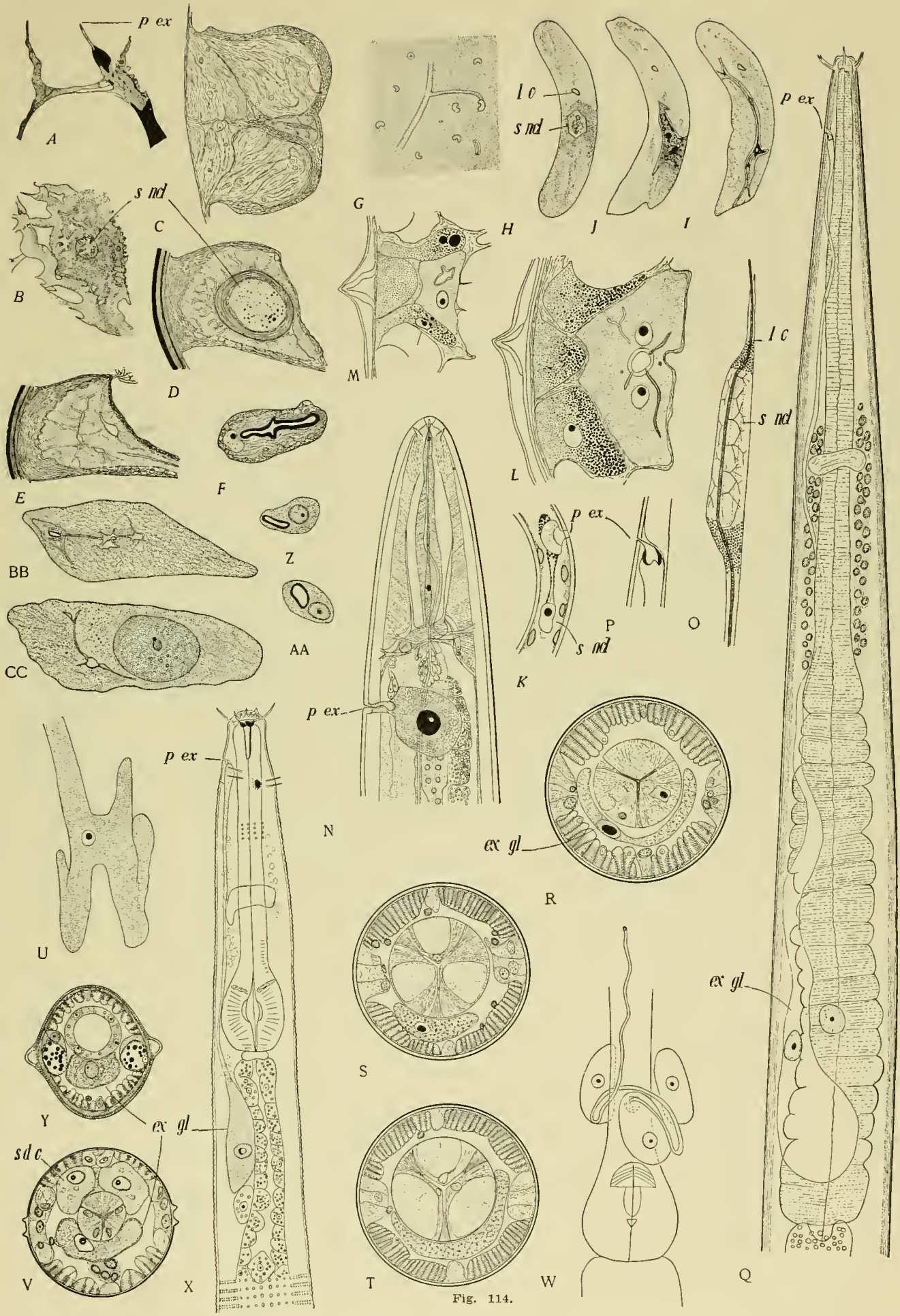
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Fig. 114.

4. Asymmetric system. A single lateral canal confined to one (usually the left) lateral chord, is apparently a reduction phenomenon which arose twice; (a) in the Ascarididae and (b) in the Tylenchoidea.

(a) Shift of the sinus nucleus to the left lateral chord in *Ascaris* with submergence of the sinus to a minor role supplies a clue as to the origin of the anisakid system. Representatives of this group have been studied by Mehlis (1831), v. Siebold (1838), Schneider (1866), Cobb (1888), Hamann (1895), Jägerskiöld (1893, 1894, 1898) and Mueller (1927). In such forms the excretory pore is often situated far forward, even between the subventral lips (*Anisakis simplex*). The system as observed in *Contracaecum* and *Anisakis* consists of a terminal duct connected with a lateral canal in the left lateral chord, this canal being greatly enlarged and having numerous side branches (Fig. 114 O). As in *Ascaris*, branching is most noticeable at the level of the gigantic sinus nucleus. According to Jägerskiöld and Mueller the entire system consists of a single cell served by the one large nucleus (Fig. 114 H-J), but this seems improbable in the light of other observations which have shown that the terminal duct is a separate entity.

Hamann (1895) found an even greater reduction in the excretory system of *Goezia annulata*. Here the entire system is formed by a short tube (Fig. 113 OO-PP) which begins in the left lateral chord and ends between the subventral lips. This tube is composed of three cells in tandem, the lumen being intracellular.

4b. The tylenchoid system (Fig. 9C) was first noted by Davaine (1857) and later observed by Bütschli (1873), Strubell (1888), Debray and Maupas (1896), and Cobb (1914). Unlike the situation in the Anisakinae, there is no shift anterior of the excretory pore correlated with asymmetry. In these forms there is a very well developed, long terminal duct leading posteriorly to one lateral chord. This chord may be either right or left, usually right but the side varies not only with species and strains but also among individuals of a given population. The terminal duct apparently has one small nucleus in its wall and the lateral canal contains a gigantic sinus nucleus (Fig. 113 H). Tylenchoids also differ from Anisakinae in that the lateral canal extends anteriad to its junction with the terminal duct. Cobb (1914) described in this group the only nema thus far known with a posterior ventral excretory pore, *Tylenchulus semipenetrans*, and in this form there is sexual dimorphism, the excretory pore being near the middle of the body in the male.

There is no evidence of relationship between these two asymmetric systems any more than there is between the forms grouped under the inverted U system or the H system. Undoubtedly we would derive 4a from 3 (ascarid) and that from 1b just as 4b would be derived directly from 1a.

Adenophori (Aphasmidia)

Thus far, only one type of non-canalicular excretory system is known, that being the simple ventral gland cell as first observed by Eberth (1863) in *Oncholaimus*, *Enoplus* and *Enchelidium*, (*Enoploidea*). Shortly thereafter Bastian (1866) described the same type of cell in *Cyatholaimus* (Chromadoroidea) and *Sphaerolaimus* (Monhysteroidea). Since then through the work of de Man, Cobb, Steiner and others, we have come to view this as the typical aphasmidian system. In it there is often a terminal ampulla (Fig. 112 O-P) and the excretory cell may have a greatly elongated neck (Fig. 114 Q) but it is never lined with a cuticle except at the terminus. It might be regarded as corresponding either to the sinus cell or the terminal duct cell. Because of the absence of lateral canals, which we associate with the presence of a sinus cell, we prefer the latter interpretation. According to this view the terminal duct cell of the Secernentes system is homologous to the ventral gland of the Adenophori. In chromadorids and desmodorids there are often one or more small elongate bodies posterior to the excretory cell which have been considered secondary or auxiliary excretory cells (see Steiner, 1916) but more recent study has shown them to be coelomocytes without apparent protoplasmic connection with the excretory system.

De Man (1886) found the ventral gland of *Enoplus communis* to be lobed in such a manner as to justify the term H-shaped (Fig. 114 U). Some more recent workers such as Wülker and Stekhoven (1933) have interpreted the structure found in *Enoplus*, as an early stage in the origin of the H-type excretory system. The writers regard the lobation in *Enoplus* a coincidence since it would not account for the existence of a cuticularly lined terminal duct. The typical ventral gland has been described in representatives of the Chromadoridae (Fig. 114 X), Microlaimidae, Cyatholaimidae, ? Desmodoridae, ? Epsilonematidae, ? Draconematidae, Camacolaimidae, Axonolaimidae, Comesomatidae, Monhysteridae, Linhomoeidae, Enoplidae, Oncholaimidae, and Ironidae. There is scarcely a group, however, in which a ventral gland has been found in all genera. Perhaps this is due to delicacy of the tissue which changes quickly on fixation. We have been unable to locate a ventral gland cell in *Ethmolaimus revaliensis*, *Monoposthia hexalata*, *Monhystera cambari* and *Theristus setosus* even after careful examination of serial sections.

Jägerskiöld (1901) associated the existence of sublateral hypodermal glands with degeneracy of the excretory system in aphasmidians in general and *Cylicolaimus magnus*, *Thoracostoma* spp. and trichuroids in particular. While it is true that hypodermal glands are very well developed in some such forms, they are no more so than in species with a distinct ventral gland such as *Acanthonchus viviparus* (Fig. 15 N). Furthermore, sublateral hypodermal glands are now being found in more and more groups in which they had been overlooked (linhomoeids, oncholaimids, dorylaimids, microlaimids, chromadorids).

Nevertheless, it seems to be an established fact that no excretory system is present in either the Trichuroidea or Dioctophymatoidea (Linstow's Pleuromyarii; Rauther's Hologonia). In the related Dorylaimoidea ordinarily no excretory pore may be observed but a rudimentary pore has been mentioned by some authors and de Coninck (1931) illustrated a terminal excretory duct connected with a ventral gland cell in *Diphtherophora vanoyci*. A similar arrangement is indicated for the Mermithoidea in which an excretory pore and terminal excretory duct is commonly attributed to pre-parasitic and young parasitic mermithids (Fig. 93). In adult mermithids usually no pore is to be observed, but forms in which the structure has persisted have been described by Rauther (1909), and Steiner (1919). Corti (1902) described in *Hydromermis rivicola* an excretory canal in one lateral chord but no excretory pore was observed and the structure was not illustrated. Hagmeir (1912) described and figured the ventral gland devoid of any terminal duct in adult *Mermis brevis*, and the writers observed a similar structure in *Hydromermis* sp.

The families Tripylidae and Mononchidae resemble dorylaimoids in that the excretory system is usually inconspicuous or overlooked. Cobb (1918) established the existence of an excretory pore in *Mononchulus ventralis* and the writers have seen such in sections of *Prionchulus muscorum*. As yet the internal connections of the excretory tube have not been determined.

The excretory system of plectids remains to be discussed. As in so many other characters, so here also, the plectids show greater resemblance to the rhabditoids than to any other phasmidians. The conception of the excretory system of plectids has been confused considerably by interpretations. The odd loop of the terminal duct (Fig. 112 N) gave the genus its name. At the level of this loop there are a large ventral gland cell and two dorsal cells (Fig. 114 W). We have previously (see Fig. 15 A) conceived the terminal duct as entering the two subdorsal cells but this seems to be wrong; it enters only the ventral cell. The only suggested function of the other two cells is athrocytic. It should be noted that *Anaplectus* and *Plectus* have no lateral canals though they have a well developed terminal duct; whether or not the duct itself has its own nucleus in addition to the gland nucleus we cannot say. *Anonchus mirabilis* provides another and even more interesting bit of evidence as to the evolution of the excretory system for in it one finds an inverted U-shaped system *in the body cavity* and not in the lateral chords; in this instance there is a distinct terminal duct, apparently with a separate nucleus, and a large sinus cell from which two apparently solid protoplasmic appendages extend pos-

teriorly through the body cavity. For the time being, *Anaplectus* and *Plectus* might be considered aberrant offshoots while *Anonchus*, by slight transformation, could account equally well for the origin of the Adenophori system as for the Secernentes system. Thus, again we find the Plectidae holding the key to points in nemic evolution.

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CHAPTER X
THE REPRODUCTIVE SYSTEM

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Introduction

The reproductive system is more or less similar in both sexes of all nematodes, being composed of one or two (rarely multiple) tubular gonads, each gonad being comparable to a single testicular or ovarial tubule of arthropods or vertebrates.

Sexual dimorphism is, as a rule, limited to characters of the reproductive system such as the vulva and male copulatory apparatus (bursa, spicules, genital papillae) but it is manifested to a minor extent in the fact that females are nearly always larger than males. Among the parasitic species this tendency becomes most marked in *Trichosomoides crassicauda* in which the male is so small that it enters the female by way of the vulva and spends its life within the uterus (Fig. 115 D). Other marked but less spectacular cases are those of *Dracunculus medinensis* and *Philometra globiceps* in which the female becomes 18 and 33 times as large, respectively, as the male. In these cases, however, the female continues growth after copulation takes place. *Howardula benigna* (Allantonematidae) presents a similar case of copulation in a juvenile stage but afterwards the young female enters a new host where it undergoes the greater part of its development.

Sexual modifications of gross body form are rare and usually take a single course, the enlargement of the female so that she becomes a reproductive sac—*Heterodera* (Fig. 115 N), *Tetrameres* (Fig. 115 C), and *Tylenchulus*. The lobes of *Phlyctainophora* may only be the result of growth in a confined situation. The Allantonematidae (inhabiting the body cavity of insects) present more examples of reproductive sac formation than do all other nemic groups combined. In this group we find *Tylenchinema* (Fig. 115 J), *Chondronema*, *Scatonema* (Fig. 115 E), and *Allantonema* (Fig. 115 I) all of which show progressive stages of degeneration of the female to reproductive sac formation. *Tripius* (Fig. 115 K) and *Sphaerularia* (Fig. 115 A-B), of the same family, go much further in degeneration; after copulation of the precocious free-living adults the females enter the new host and growth of the reproductive system takes place at the expense of the remainder of the body. The uterus with the ovary enclosed is everted and continues to grow until it is many times as large as the female body.

Most of the remaining types of sexual dimorphism are attributed to failure of the male to attain complete development, such are the sexual differences in cephalic characters, esophagus, and cuticle of thelastomatids. Seurat (1920) considered the alae and spines of the male of *Tetrameres fissispina* as organs of propulsion and fixation necessary to its free life in the succenteric ventricle of its host and migration to the female, which lives sedentarily in the gastric glands of its host. Sexual dimorphism in free-living nemas is extremely rare, the most outstanding examples being members of the Enchelidiinae; in some of these forms there may be complete degeneration of stoma in the adult male (*Enchelidium pauli* Fig. 63 I-J). In male tylenchoids, the stylet is often not as well developed as that of the female, *Hexatylus abulbosus* (Syn. *Neotylenchus abulbosus*) being an extreme example of this type of dimorphism. Sexual dimorphism in size of amphids, those of the male being the larger, has been described in such forms as *Trilobus gracilis* var. *homophysalidis*, *Ironus ignavus* and some mermithids.

Intersexes. Meissner (1853) first observed male secondary sexual characters (spicules and genital papillae) in normal female *Hexamermis albicans*. Such forms were erroneously regarded as hermaphrodites but this is a false impression as only one set (female) of reproductive organs is developed. Since the time of Meissner such intersexes have been described in *Enoplus communis* (syn *E. cochleatus*) by Schneider (1866), in *Chromadora poecilisoma* and *Thoracostoma figuratum* by de Man (1893), in *Porrocaccum heteroura* by Willemoes- Suhm (1869), in *Tribolus diversi-papillatus* by Daday (1905), *Trilobus gracilis* by Ditlevsen (1911), W. Schneider (1922) and Linstow (1903). Hagmeier (1912), Steiner (1923) and Christie (1929) have described intersexes in mermithids. The latter author found that sex is determined by the number of parasites in a host. When one to three parasites were present in grasshoppers they were females, when four to 23, they were mixed, and when above 23 they were all males. By feeding a known number of parasite eggs to the host, Christie determined that the sex ratios were not due to selective mortality. The fact that intersexual males are unknown seems to cast doubt upon the theory that the sexes are primarily present in equal numbers and may be converted to the opposite sex by the influence of environmental factors. Nevertheless, intersexes seem to be related to crowding and when a single female is present in a host containing 10 males, it is conceivable that they might cause her to be an intersex.

General Morphology

So long ago as 1866 Bastian remarked on the difference between the reproductive systems of free-living and parasitic nemas; he felt that the relative simplicity of the system in free-living nemas was sufficient ground for the separation of that group from parasites as a separate family (Anguillulidae, equivalent in scope to our Rhabditina, Chromadorida, Enoplina and Dorylaimoidea). The greater complexity of the reproductive system in parasitic nemas is chiefly limited to the female sex and is correlated with increased egg production.

Division of the nemas into taxonomic groups on the basis of the reproductive system has been proposed by only one modern author, Rauther, (1918, 1930) who divided the Class Nematoda into two orders: Telogonia (includes Phasmidia, Chromadorida, Enoplina, Dorylaimoidea and Mermithoidea) and Hologonia (Trichuroidea and Dioctophymatoidea). These divisions apply to both sexes. The germinal zone in the order Hologonia (examples *Trichuris trichiura* as observed by Eberth, 1869, and *Dioctophyma renale* as observed by Leuckart, 1876, (p. 378) extends the entire length of the gonad, being composed of a series of germinal areas on one side of the gonoduct in the former and comprising the entire circumference of the gland in the latter. In neither case is a rachis present and the entire group Hologonia is characterized by the presence of a single gonad in both sexes. In the majority of nemas (Telogonia) it is a well established fact that new germ cells originate only at the end of the gonad. However, only a small proportion of the Nemata (particularly parasites) has been well studied from this standpoint. Data regarding mermithids and *Cystoopsis* should be particularly informative but are lacking to date.

Eschricht (1848) discovered that in the female ascaridids germ cells are not free in the gonoduct but are grouped around a central axis which is termed the rachis. Subsequent authors have found this structure to be a common feature of ascaridids, oxyurids, strongylins, and spirurids. Some, including Bütschli, compared the rachis to the cell of Verson or apical cell of the gonads of insects, but as pointed out by Seurat (1920) the rachis is not a constant feature of nemas even in special groups, (it is present in *Bradynema*, absent in *Ditylenchus*) and it does not supply yolk, for the nucleus and protoplasm grow in the same proportion as the oogonium passes down the tube. The function of the rachis is not understood and its apparent erratic occurrence seems to eliminate it as an ordinal character.

The genital primordium is identical in that it consists of two germ cells and two epithelial cells in the first stage larva of both sexes of all nemas studied. In forms with two gonads the primordial germ cells are thereafter separated by somatic cells, one germ cell entering each gonad, while in forms with one gonad the germ cells remain together. In two-ovaried forms the intervening cell group forms the two uteri and connects with the vagina in the female, or forms the vas deferens in the male. It would therefore, seem obvious that two gonads

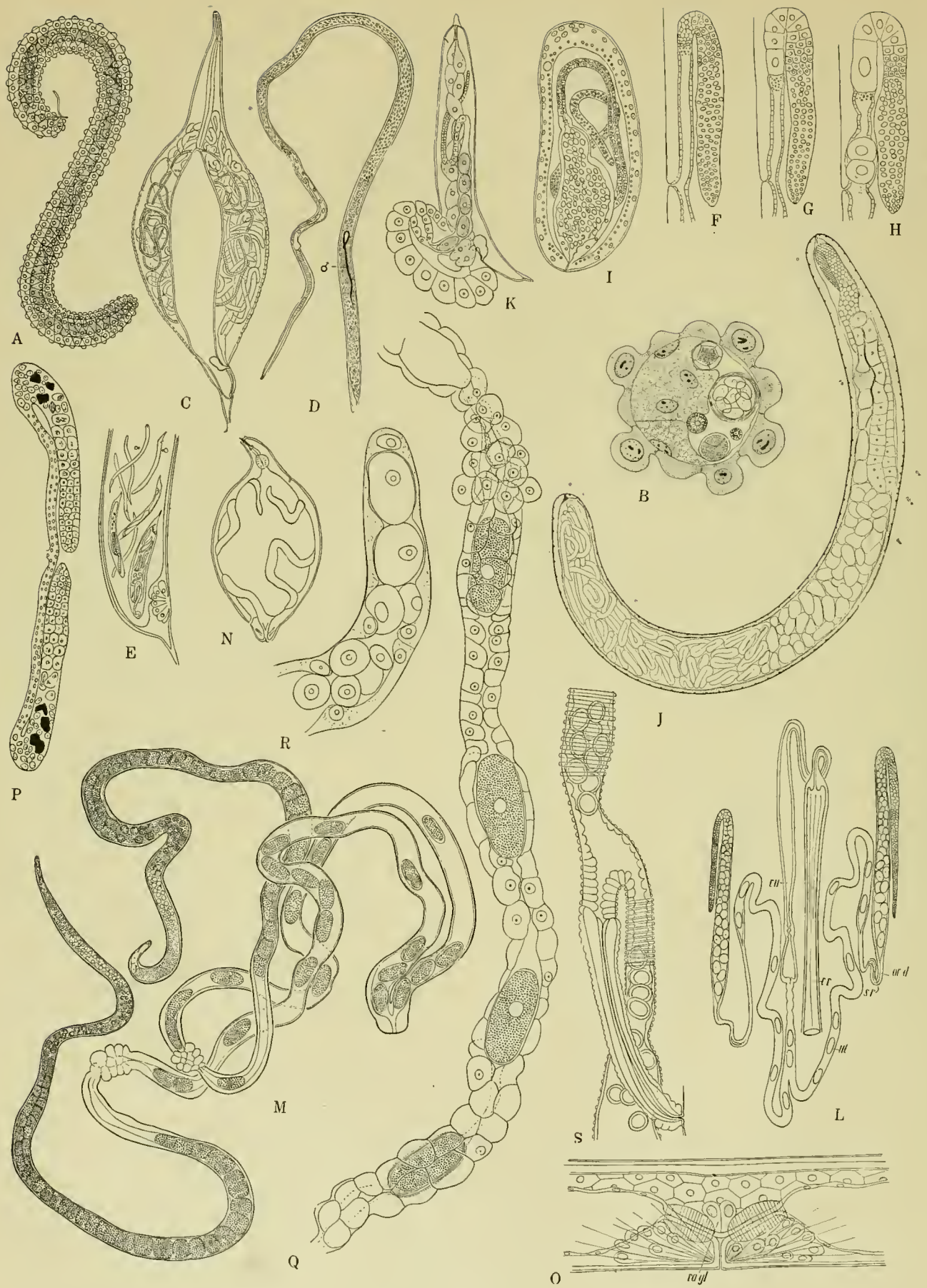

Fig. 115.

are the primitive nemic condition. Bütschli (1876), Steiner (1919, 1920) and Seurat (1920) have taken the view that parallel posteriorly opening gonads are primitive for both sexes in nemas. Such a condition is a contradiction to what we know of free-living nemas. First, parallel ovaries are known to occur in only one genus, not parasitizing vertebrates, said genus being the highly specialized plant parasite, *Heterodera* (Fig. 115 M). Second, parallel testes are known to occur in only two genera, *Anticoma* (Fig. 124 L) in which the parallel condition appears to be a modification of the opposed condition and *Hetcrodera marioni* in which the paired testes seem to have arisen secondarily as a longitudinal splitting of a single testis (see p. 150). Otherwise, wherever two gonads are present in free-living nemas, they are opposed. Without venturing further in the matter of primitivity at this time (see also p. 195) the following points seem notable: Admitting that from the standpoint of general comparative anatomy the paired gonads of both sexes should have opened posteriorly into the ventral side of the cloaca, the ontogeny of present day nemas indicates that in the original nema the vulva was separate and equatorial. Any other arrangement must have occurred prior to the origin of the class.

Since the female reproductive system is more often used in systematics and since more observations have been recorded in more diverse groups it shall be considered first.

Female Reproductive System

GROSS MORPHOLOGY

Seurat (1913-1920), in a series of papers culminating in his "Histoire Naturelle des Nématodes de la Berbérie", developed an extremely useful nomenclature for the parts of the female reproductive system and at the same time presented more useful information on this subject than all other workers combined. Seurat was fully aware that the groups formed by his classification of the female reproductive system were artificial and he himself pointed out the numerous transitions from one of his major groups to another, within families and genera. His classification was as follows:

I. Uteri opposed. Amphidelphes:

1. a: *Dictyocaulus filaria* (Metastrongylidae). Vagina short, uteri opposed, oviducts U-shaped, ovaries converging (Fig. 116 Q).

b: *Allodapa numidica* (Heterakidae). Similar to 1a but with longer vagina, and uteri twice reflexed in U-shape.

c: *Camallanus microcephalus* (Camallanidae). Similar to 1a but with longer vagina, and posterior gonad represented by a blind uterine sac, posterior ovary and oviduct absent (Fig. 117 H).

2. *Heterakis* (Heterakidae). Vagina much elongated, U-shaped; uteri opposed, reflexed; ovaries much contorted (Fig. 116 R).

3. *Haemonchus* (Trichostrongylidae). Vagina short; anterior uterus and ovary extending anteriad; posterior uterus U-shaped; posterior ovary also anterior to vulva (Fig. 116 T).

4. *Trichuris* (Trichuridae). Anterior genital tube totally absent; posterior uterus extending nearly to posterior extremity; oviduct U-shaped extending nearly to vulva where it is again reflexed; ovary much coiled, extending length of body (Fig. 117 F).

5. *Acuaria laticeps* (Acuariidae). Uteri opposed, very long, serving to contain a mass of many small eggs; oviducts and ovaries very filiform, oviducts entering uterus in esophageal and preanal regions (Fig. 116 P).

6. *Protrellus* (Thelastomatidae). Vulva shifted anteriad; vagina greatly elongated; uteri opposed (Fig. 116 K).

7. One-ovaried forms with the vulva posterior. *Acuaria invaginata, Heligmosomum laeve, Atractis dactylura* (Fig. 117 E).

II. Uteri parallel.

A. Opisthodelphes. Uteri directed posteriad; vulva usually anterior to middle of body.

8. *Ascaris lumbricoides.* Vagina short; uteri directed posteriad; oviducts and ovaries much contorted (Fig. 117 L & T).

9. Physalopterids, thelaziids, and filariids are usually opisthodelphic; the ovaries coiled in the preanal region.

10. *Maupasina.* Vulva situated in anal region; uteri directed anteriad, turn posteriad and terminate in two parallel ovaries in posterior region.

B. Prodelphes. Uteri directed anteriad.

(a) Original or primitive prodelphy.

11. *Dermatoxys.* Seurat considered the oxyurids the most primitive group and characterized them as for the most part prodelphic but with variably situated vulva. (Fig. 117 W).

(b) Secondary prodelphy.

aa) Vulva near anus.

12. *Chabertia.* Uteri extending anteriad. Ovaries coiled in anterior part of body. Type obviously a modification due to posterior shift of vulva of the amphidelphic type found in trichostrongyles.

13. *Tetrameres.* Uteri narrow, parallel and very long; oviducts and ovaries filiform, entwined around the uteri in the esophageal region (Fig. 117 I).

bb) Vulva anterior

14. *Aprocta orbitalis.* Genital tubes parallel, U-shaped, descending posteriad then reflexed anteriad where they terminate in oviducts and ovaries entwined in the cephalic region.

Today, Seurat's terminology is accepted in general and adjectives derived therefrom are applied widely in taxonomic descriptions. Because of the difficulty in tracing uteri and ovaries certain arbitrary limitations of definition have come to be accepted. Thus, *amphidelphic* is redefined as having uteri opposed at origin regardless of location of oviducts or ovaries. Similarly, *prodelphic* is defined as having uteri parallel and anteriorly directed at origin while *opisthodelphic* is defined as having uteri parallel and posteriorly directed at origin.

Other adjectives also introduced by Seurat, Ortlepp and Schulz were as follows: *Monodelphic*, meaning: provided with one complete genital tube. (Because of variability in the degree of development of a second uterus and ovary in such forms, this word has come to be applied to the ovary. Thus, *Camallanus* and *Atractis* are now both considered monodelphic prodelphic). *Didelphic* meaning: provided with two complete genital tubes; forms may be didelphic opisthodelphic or didelphic amphidelphic. *Tetradelphic*, meaning: provided with four complete genital tubes; *Polydelphic* provided with more than four complete genital tubes.

Parts of the Reproductive System. Seurat (1920) like Bastian (1866) noted the morphologic difference between the vagina and uteri of free-living nemas and those same structures of parasites. Primarily the genital tubes in females (Fig. 3) of free-living nemas consist of *vulva*, simple transverse *vagina*, paired opposed *uteri* without heavily muscled areas, short sometimes indistinct oviducts and short tubular *ovaries*. A definite seminal receptacle or spermatheca may be developed as an outpocketing of each uterus (Fig. 116 A) or oviduct; in other forms its function is assumed by the ovarial end of the uterus (Fig. 116 B, F & G). As noted by Filipjev (1918, 1922, 1929, 1934) the ovaries are outstretched (Fig. 116 L-N) in some large groups and reflexed (Fig. 116 C-F & O) in other large groups. Actually the ovaries themselves are seldom reflexed in free-living nemas, more commonly the flexure occurs at the junction of ovary and uterus, or of ovary and oviduct.

Vagina and Uteri. With parasitism there is generally an increase in length of the entire genital tube with coincident increased egg production, and increase in

Fig. 115

Female reproductive system. A-B—*Sphaerularia bombi.* C—*Tetrameres fissispina.* D — *Trichosomoides crassicauda.* E—*Scatonema wuelkeri.* F-H—*Rhabditis sechellensis* (F, during sperm formation; G and H, later stages). I—*Allantonema mirabile.* J—*Tylenchinema oscinellae.* K—*Tripius gibbosus.* L—*Macracis monhystera.* M, Q-R—*Heterodera marioni* (M, entire female reproductive system R, blind end of ovary; Q, upper part of uterus, all as seen in specimen dissected in egg albumen). N—*H. schachtii.* O—*Thoracostoma strasseni.* P—*Rhabditis aspera* v. *aberrans.* S—*Aplectana gigantica,* vagina showing origin of uteri and structure of ovejectors. A-B and K, after Leuckart, 1887, Abhandl. Math.-phys. Classe, Konigl. Sachs. Gesellsch. Wiss. v. 13 (8); C, after Travassos, 1919, Mem. Inst. Oswaldo Cruz, v. 11; D, after Hall, 1916, Proc. U. S. Nat. Mus. v. 50; E, after Bovien, 1932, Vidensk. Medd. Dansk. Naturh. Foren., v. 94; F-H, after Potts, 1910, Quart. J. Micr. Sc., v. 55 (3); I, after Wuelker, 1923, Ergeb. u. Fortsch. Zool., v. 5; J, after Goodey, 1930, Philosoph. Tr. Roy. Soc. Lond. s. B. v. 218; L, after Rauther, 1918, Zool. Jahrb. Abt. Morph., v. 40; N, after Strubell, 1888, Bibliotb. Zool., v. 1 (2); O, after Turk, 1903, Mitt. Zool. Stat. Neapel, v. 16; P, after Kruger, 1913, Ztschr. Wiss. Zool., v. 105 (1). Remainder original.

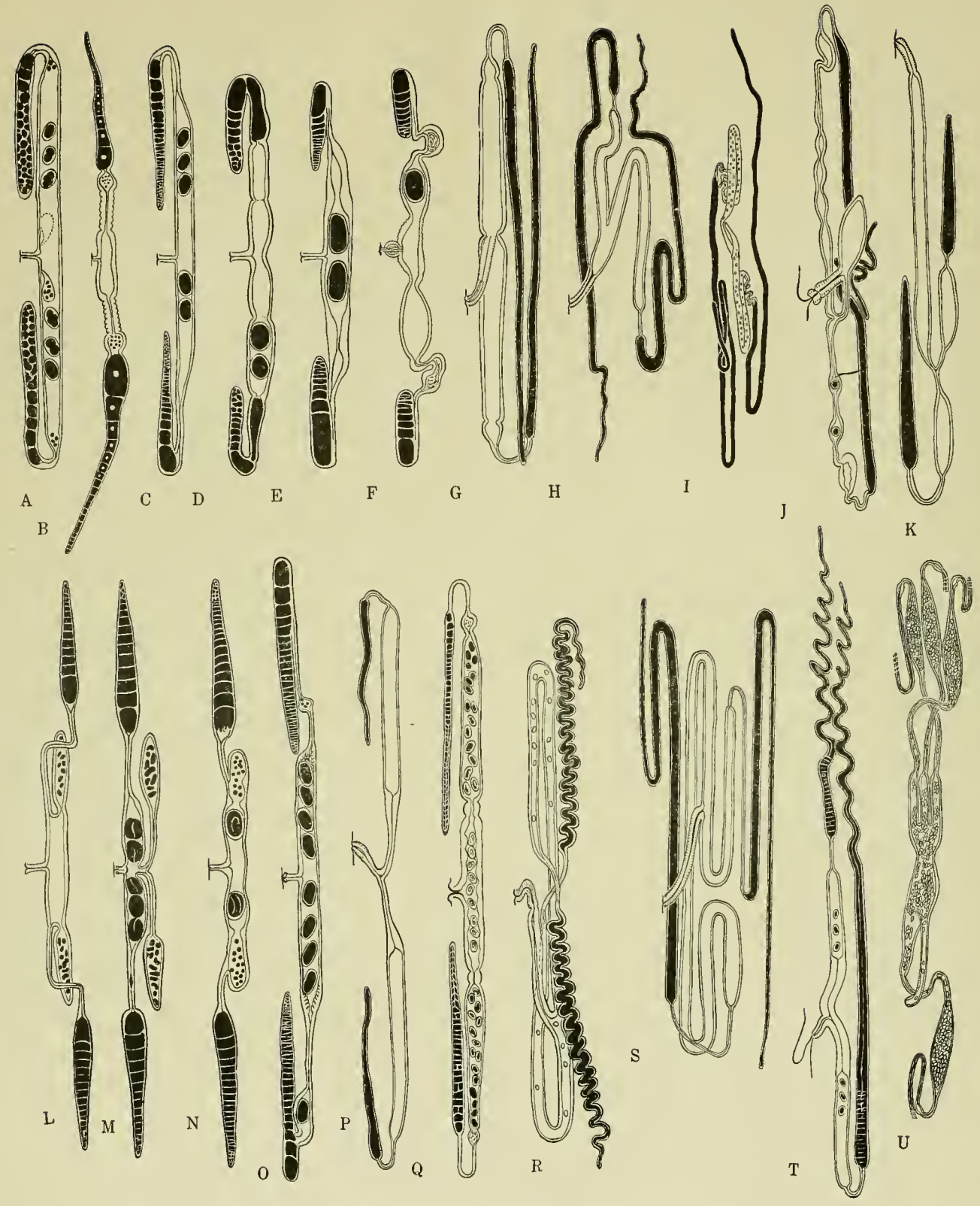

Fig. 116. DIAGRAMS OF FEMALE REPRODUCTIVE SYSTEM.

A—*Rhabditis strongyloides;* B—*Tylenchorhynchus dubius,* C—*Anaplectus granulosus.* D—*Chromadora* sp. E—*Mononchus lacustris.* F—*Trilobus pellucidus.* G—*Cephalobellus papilliger.* H—*Cucullanus mirropapillatus.* I—*Aplectana gigantica.* J—*Rhigonema infectum.* K—*Protrellus kuenckeli.* L—*Doryloimopsis metatypicus.* M—*Sabatieria hilarula.* N—*Axonolaimus spinosus.* O—*Actinolaimus sp.* P—*Acuaria laticeps.* Q—*Dictyocaulus filaria.* R—*Heterakis gallinae.* S—*Spironoura affine.* T—*Haemonchus contortus.* U—*Tanqua tiara.*

B, after Goodey, 1932, J. Helminth., v. 10 (2-3); H, after Toernqnist, 1931, Goteborgs Kungl. Vetensk . . . s. B v. 2 (3); K, after Schwenk, 1926, Sc. Medica v. 4; L after Olsen, 1938, Tr. Am. Micr. Soc., v. 57 (2); P, after Senrat, 1920, Histoire naturelle . . . ; Q, after Augstein, 1894, Arch. Naturg. 60J., v. 1 (3); R, after Baker, 1936, Tr. Roy. Canad. Inst. v. 21 (2); U, after Monnig, 1923, 9 & 10th Rpt. Director Vet. Education & Res. Remainder original.

muscular development of uteri and vagina for the ejection of the eggs. The vagina (lined with cuticle) commonly becomes elongated to the form of a muscular tube. This tube may connect directly with the bifurcation of the uteri (Fig. 119 A & B), or it may be followed by a non-ectodermal tube of similar construction (Fig. 115 L). In the latter case the second section is termed the *vagina uterina*, the first section, *vagina vera*. The functional term *ovejector* was applied to the entire thick-walled terminal part of the reproductive system by Seurat. In some nemas (*Nematodirus*, Fig. 118 BB-DD) the ovejector bifurcates. The three parts of each ovejector were named by Maupas and Seurat (1912), vestibule, sphincter, and trunk (Trompe). Later, (1920) Seurat revised his terminology, then calling the three parts of the strongylin ovejector *vestibule, glazing gland* [Firnissdrüse of von Linstow (1878)] and *sphincter*. These parts correspond to ovejectors 1, 2 and 3 as described by Ransom (1911) and *pars haustrix* and *pars ejectrix* as described by Looss (1905). It is unfortunate that such confusion has occurred. The application of functional terms is always likely to lead to such. However, since the ovejector is itself a functional rather than a structural entity, we must continue at least some of the terminology. As revised by Seurat, the *trompe* is sometimes equivalent to the vagina uterina (praeuterus of Rauther, 1918) being the undivided part of the uterus in *Ascaris, Gongylonema, Spirura* (Figs. 117 L, 118 GG-KK & 118 N-O). It may also become a divided thick walled non-cuticular part of the ovejector as in *Habronema microstoma* (Fig. 118 P) and finally it may exist both in divided and undivided parts as in *Protospirura numidica*. Attempts to homologize parts on the basis of gross appearance lead to little of value. In some forms such as *Gongylonema scutatum* the vagina vera constitutes the major part of the ovejector and it is separated by a constricted region, i. e., sphincter, from the shorter vagina uterina (Fig. 118 KK). In the same genus in *G. mucronatum* the vagina vera is extremely inconspicuous, no sphincter is present, and the major part of the ovejector is vagina uterina. Undoubtedly such specializations as sphincters are of multiple origin and we see no advantage in renaming the functional sphincter of the strongyle ovejector, glazing gland (Fig. 118 CC-ovj. 2).

In parasites, as also in free-living nemas, monodelphic forms commonly have a postvulvar uterine sac (Fig. 117 H) which functions as a *seminal receptacle* or *spermatheca*. Such a uterine sac is considered the remainder of a second genital tube. In others (*Tetrameres fissispina*) a separate sac is formed as an outpocketing of the vagina vera (Fig. 118 G). More often, the distal ends of the uteri are more or less distinctly modified as seminal receptacles.

Oviduct. This part of the system is less likely to be confused than other parts. However, like other parts it is a functional rather than a structural entity, i. e., a constricted thick-walled region between uterus and ovary. In *Rhabditis strongyloides* (Fig. 3) it is hardly an entity while in *Sabatieria* (Fig. 120 B) and *Anaplectus* (Fig. 120 C) it is clearly differentiated. In the parasites it attains its greatest development in oxyurids such as *Syphacia obvelata* (Fig. 159 K-L) and occasionally, as in this form, a dilation of the oviduct serves as a seminal receptacle. Vogel (1925) was led by these structures to believe the oviduct functioned as egg former (see chapter XII).

Ovary. In telogonic forms each ovary consists of (1) a germinal zone and (2) a growth zone. The latter commonly becomes the major part of the gonad in parasitic nemas.

Abnormalities. Bivulvar specimens have been recorded by Bütschli (1874) in *Linhomoeus mirabilis*, Paramonov (1926) in *Trilobus gracilis* and Cassidy (1928) in *Dorylaimus* sp. Cassidy (1933) later recorded a specimen of *Prionchulus muscorum* with three ovaries and uteri, the third being connected with the second vulva. Chandler (1924) recorded a specimen of *Ascaris lumbricoides* with three uteri and ovaries. These must all be considered monstrosities.

DETAILED MORPHOLOGY

The minute anatomy of very few nemas has been adequately investigated. Those who have been major contributors to this subject are as follows: Nelson (1852), Bischoff (1855), Meissner (1855), Thompson (1857), Van Beneden (1883), Nussbaum (1884), Vogt and Jung (1888), Wasielewski (1893), Sala (1904), Domaschko (1905), Scheben (1905), Looss (1905), Kemnitz (1912), Romeis (1913), Zacharias (1913), Maupas and Seurat (1912), Seurat (1920), Maupas (1899), Pai (1927, 1928), Musso (1930), Baker (1936) and Mackin (1936). The major part of this work has been done on *Ascaris lumbricoides* and *Parascaris equorum*; less comprehensive studies have been made on other species.

(a) *Ovary.* The ovary consists of a tubular sac in which germinal cells develop. This sac consists of an epithelial layer and a germinal chord. In most nemas with the exception of hologonic forms, germinal elements do not arise from the epithelium. The epithelium consists of a single layer of greatly elongate, flat (simple squamous), spindle-shaped cells which reach 1 meter in length in *Ascaris lumbricoides* according to Musso (1930); each of these cells is multinucleate; as they near the oviduct they become shorter until they are only 2 mm. in length and have 12 to 20 nuclei (Fig. 121 N-O). Such astounding size is apparently a proportional development in keeping with the general oversize structure of *Ascaris*. The cells show the same spindle-shape but are not spectacularly long in *Spironoura* (Fig. 122 H).

In general the gonad is divisible into two regions, as follows: (1) The germinal zone: An area of rapid division of relatively small cells, often not showing clear cell boundaries. (2) The growth zone: An area of gradual increase in size of the oogonia. The first of these zones is always relatively short while the latter varies tremendously in size, sometimes amounting to the greater part of the gonad length, as in *Ascaris lumbricoides*. Although a conspicuously long growth zone is usually associated with parasitism, it is by no means limited in occurrence, being found likewise in such forms as *Metoncholaimus*.

At the blind end of the ovarial tube the epithelium becomes extremely thin so that its very existence has been denied by some authors, while others have concluded that the large *cap cell* is the epithelial cell of the ovarial terminus. This viewpoint has been questioned by Musso (1930) who regards the cap cell as an undifferentiated germinal stem cell which gives rise equally to both epithelial cells and germinal cells. In accord with the majority of observers, the writers have never seen any sign of nuclear division in a cap cell. Also, we find the protoplasm of the germinal chord rather clearly segregated from this cell in *Spironoura* (Fig. 122 G). With Maupas (1899) and Pai (1927) the writers would conclude that the cap cell is a part of the ovarial epithelium. Cell borders are often difficult to distinguish at the proximal or germinal end of the germinal chord, but sometimes they are distinct and it seems proper to regard the region as cellular rather than syncytial in all instances, since cell boundaries gradually become more apparent as the cells move down the gonoduct.

The origin and significance of the rachis is as yet unsettled. Beginning at a slight distance from the extreme end of the germinal chord one finds a central strand of non-nucleated tissue which extends in *Ascaris* to the beginning of the oviduct. It would seem that there are two possible origins of the rachis, one as a continuation and product of the cap cell, the other as a residuum of enucleated plasma separated off from a germinal syncytium. Either assumption has lacked evidence. Earlier authors (Bütschli) leaned to the opinion that the rachis of nemas was comparable to the rachis found in the telotrophic insect ovary; such a view would require that it be a feeding mechanism and that it contain nuclei (nurse cells). Von Kemnitz (1912) found that the chief stored nutrient material of ascarid oogonia is glycogen and that this substance is absent from the rachis throughout the germinal region, only making its appearance in that structure *after* it has become the most conspicuous feature of the oogonium. Von Kemnitz traced the distribution of glycogen in the gonad demonstrating conclusively that it is first seen in the epithelium of the upper part of the ovary, thereafter, less concentrated in both epithelium and oogonia and finally absent from the epithelium, concentrated in the oogonia and scattered in the rachis. One concludes that it is obtained from the epithelium by absorption. Seurat (1920) pointed out that increase in nuclear and plasmatic size in the growth zone is fairly proportionate, which would not be the case if nurse cells or a vitelline tissue were actively contributing plasma to the oogonium. The same author

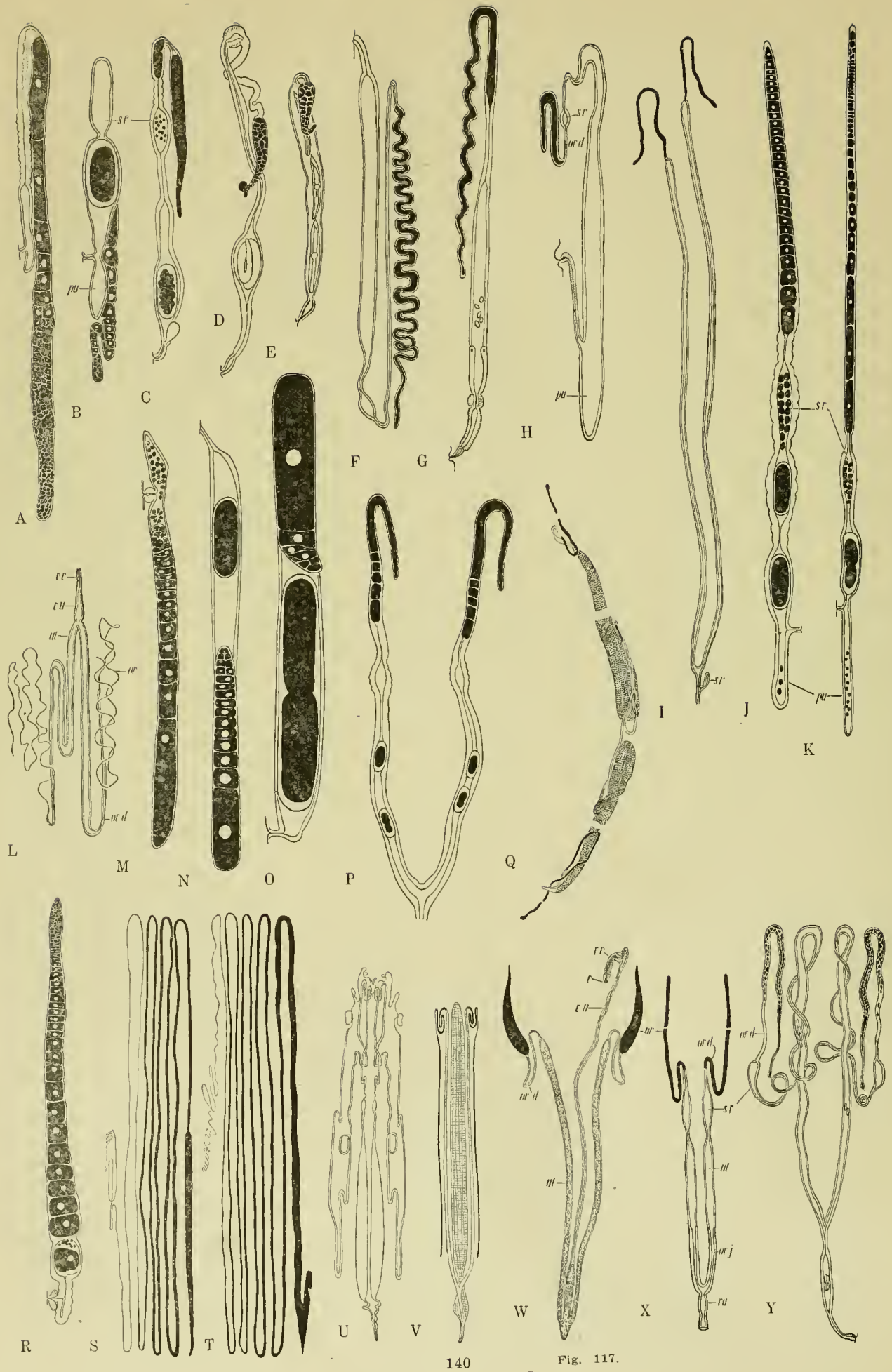

Fig. 117.

further noted that the rachis cannot be of great significance to nemas since it is often apparently absent in some species (*Macracis monhystera*) while it is present in closely related forms, (*Oxyuris equi*). Without in any way passing judgement on the function of the rachis, we may note that in some forms the growth zone of the ovary consists of a cylinder of oogonia surrounding the rachis (*Ascaris*), while in others (*Spironoura affinc*, Fig. 119, A-B) and the majority of free-living nemas) the growth zone is a single chain of cells and the rachis disappears as the oogonia assume the single file. The rachis appears in direct continuity with the cap cell in *Spironoura* (Fig. 122 G). In countless free-living nemas (ex. *Mononchus*, *Trilobus* Figs. 120 D & I-P) the germinal zone is greatly reduced in length and there seems never to be a cylindrical germ chord. In such forms no distinct cap cell or rachis is present.

(b) *Oviduct.* The oviduct, when distinct, consists of a narrow tube with high columnar epithelium. According to Musso, the oviduct in *Ascaris*, like the ovary, is devoid of a muscular layer except in the zone approaching the uterus. Rauther (1918) described a muscular sphincter at the ovary-oviduct junction in *Macracis* (Fig. 115 L), and in many oxyurids the oviduct has a muscular appearance. A slight enlargement in the proximal part of the oviduct serves as a spermatheca and fertilization chamber in *Macracis monhystera* (Rauther, 1918) and *Syphacia obvelata*, (Vogel, 1925). In the latter organism (and in many other oxyurids) the ova develop their shell while in the oviduct and Vogel was of the opinion that the oviduct should be regarded as an egg former and possibly a "shell gland". In the majority of nemas (including *Macracis*, *Spironoura* and *Rhabditis*) shell formation is first visible in the proximal part of the uterus and the oviduct cannot be regarded as a zone of egg shell deposition.

(c) *Uterus.* The greater part of the uterus has a squamous epithelium covered by a muscle layer of circular and oblique fibers, the development of which varies both in localized regions of a given form and in corresponding regions in diverse nemic groups. The distal part of the uterus commonly functions as a seminal receptacle or fertilization chamber even though it is not externally set off from the remainder. In *Ascaris* the epithelium of this region consists largely of elongated, tufted cells which were regarded by Leuckart as nurse cells to the spermatozoa. Romieu (1911), Von Kemnitz (1912) and Romeis (1913) found that these cells exercise a phagocytic activity on unused aging spermatozoa. Musso (1930) has shown that the inter-locking branched muscle fibers of the seminal receptacle rather suddenly give place to more regularly arranged circular muscle fibers of the uterus proper (Fig. 121 C). In other nemas such as *Spironoura* (Mackin, 1936) the uterine musculature is obviously spiral (119 A, 122 D) rather than circular though individual muscle cells do not reach completely around the uterus. Peristaltic contraction waves passing along the spiral serve to carry the egg along without the aid of longitudinal muscle fibers. The uterus of *Enterobius* (Fig. 122 BB-CC) has a web-like musculature. Sometimes, as in *Ascaris*, (Musso, 1930) longitudinal connective tissue fibers are apparent in the external membranes which cover the uterus, oviduct, and ovary, as well as other organs bordering on the body cavity. Concerning the histology of the uterine musculature there is little to be said. Plenk (1924) erroneously attributed striation to it as to all other musculature in *Ascaris*. Actually, the individual muscle cells seem to be either platymyarian, with the fiber layer next to the epithelium, or circomyarian.

In *Ascaris* the epithelium of the uterus proper, is composed of five to six sided, low or high cuboidal or irregular epithelial cells. Van Beneden (1883) and Martini (1916) attributed a bacillary layer to the uterine epithelium in *Ascaris* and *Oxyuris* respectively but other workers have been unable to confirm such findings in these or other nemas. In *Ascaris lumbricoides* Musso found the majority of uterine epithelium cells binucleate (Fig. 121 A-B) in all specimens, other nuclear numbers being three, four, and one in order of occurrence, four nuclei being found only in comparatively young females; nuclear division was always found to be by amitosis and cell division often unequal. In many parasitic nemas such as *Ancylostoma duodenale* (Looss, 1905), *Macracis monhystera* (Rauther, 1918) and *Cephalobellus papilliger* (Chitw. & Chitw., 1933) and in most free-living nemas the chief part of the uterus has no distinct musculature. A uni-nucleate simple squamous epithelium is the rule. In *Ancylostoma duodenale*, Looss reported the uterine wall to be composed of only two cell rows. Possible cell limitation (oligocyty) in the uterine epithelium of other meromyarian nemas has not been investigated.

When an undivided portion of the uterus forms an egg pouch, as in *Ascaris lumbricoides* and *Abbreviata poicilometra* (Fig. 118 LL-MM), the epithelium and musculature are not particularly modified but when an ovejector is formed the epithelium usually becomes thicker and the musculature more highly developed.

(d) *Vagina.* The true vagina (vagina vera) of nemas is always distinctly recognizable histologically though it may be difficult, if not impossible to limit in gross study. Regardless of degree development, the vagina is lined with a distinct, well-developed cuticular layer continuous with the external cuticle but differing from this cuticle in being composed of a single layer. Its epithelium is composed of relatively few large cells usually quite distinct in appearance from the epithelium of the uterus or vagina uterina. Because of its exceedingly narrow, slit-like form the vagina of free-living nemas has not been investigated histologically, but in *Trilobus* (Fig. 120 J) we judge it to have four cells situated at the junction of vagina and uterus. With elongation of the vagina, the structure becomes more obvious and Rautner (1918) was able to identify a single group of four nuclei at its proximal end corresponding to four longitudinally oriented cells forming the entire vagina vera of *Macracis monhystera* (Fig. 122 I). Chitwood and Chitwood (1933) have found that eight cells, arranged in two tandem groups of four each, compose the vagina of *Cephalobellus* and *Hystrignathus rigidus* (Fig. 122 X) and *Spironoura affine*. This arrangement is in accord with the general tetragonal symmetry of the vagina of oxyuroids, the nuclear number eight being preserved in *Atractis* though no other semblance of symmetry occurs in the vagina of that form. In ascaridids and spiruroids there is a distinct cell limitation in the vagina, but even so symmetry and cell constancy are apparently lost; Musso records the vagina of *Ascaris* as composed of 10 to 12 longitudinal rows of polyhedral squamous epithelial cells (Fig. 121 E-F), while Rauther (1918) found the vaginal epithelium of *Trichuris* to be composed of an unlimited number of cells (Fig. 122 T-U).

The musculature of the vagina is continuous with that of the uterus and is of the same general type but may form a much thicker layer; in some groups the vaginal muscle may be several cells in thickness and cause the vagina to have a distinctly laminated appearance. The cell bodies of the muscle cells are commonly pressed out of the wall assuming a bladder-like shape. These protoplasmic masses have commonly been termed vaginal glands. Structures which cannot be so interpreted but may actually be glands have been described in *Allodapa numidica* by Seurat (1914), in *Thoracostoma strasseni* by Türk (1903), seen also in *Cylicolaimus magnus* by Jägerskiöld (1901) and *Halichoanolaimus longicauda* by Ditlevsen (1919) (Fig. 123). Their function has not been ascertained.

Fig. 117. DIAGRAMS OF FEMALE REPRODUCTIVE SYSTEMS.

A—*Panagrolaimus heterocheilus.* B—*Cephalobus persegnis.* C—*Brevibucca saprophaga.* D—*Labidurus gulosa.* E—*Atractis dactyluris.* F—*Trichuris suis.* G—*Heligmosomum laeve.* H—*Camallanus lacustris.* I—*Tetrameres fissispina.* J—*Ditylenchus dipsaci.* K—*Aphelenchoides fragariae* (Chrysanthemum strain). L—*Ascaris lumbricoides;* M—*Oxystomina cylindraticauda.* N—*Halanonchus macramphidum.* O—*Cryptonchus nudus.* P—*Heterodera marioni.* Q—*Heliconema anguillae.* R—*Theristus sentiens.* S-T—*Ascaris lumbricoides* (S, male; T, female). U—*Zoniolaimus setifera.* V—*Oxyuris equi.* W—*Dermatoxys veligera.* X—*Kiluluma brevivaginata.* Y—*Hedruris armata.*

A, after Steiner, 1935, Proc. Helm. Soc. Wash. v. 2 (2); B, after Thorne, 1937, Proc. Helm. Soc. Wash. v. 4 (1); C, after Goodey, 1935, J. Helminth. v. 13 (4); D-E, after Thapar, 1925, J. Helminth. v. 3 (3-4); F, after Rauther, 1918, Zool. Jahrb. Abt. Morph., v. 40; G, after Seurat, 1915, Bull. Sc. France & Belg. 7. s., v. 48; H, after Toernquist, 1931, Goeteborgs Kungl. Vetensk. s. B, v. 2 (3); W, after Seurat, 1920, Hist. Nat. Nem. Berberie; Q, after Yamaguti, 1935, Jap. J. Zool. v. 6 (2); R, after Cobb, 1914, Tr. Am. Micr. Soc. v. 33; S-T, after Musso, 1930, Ztschr. Wiss. Zool. v. 137 (2); U, after Cobb, 1898, Dept. Agric. N. S. Wales, Misc. Publ. No. 215; V, after Martini, 1916, Ztschr. Wiss. Zool. v. 116; X, after Thapar, 1925, J. Helminth., v. 3 2; Y, after Perrier, 1871, Compt. Rend. Acad. Sc. v. 72 (12). Remainder original.

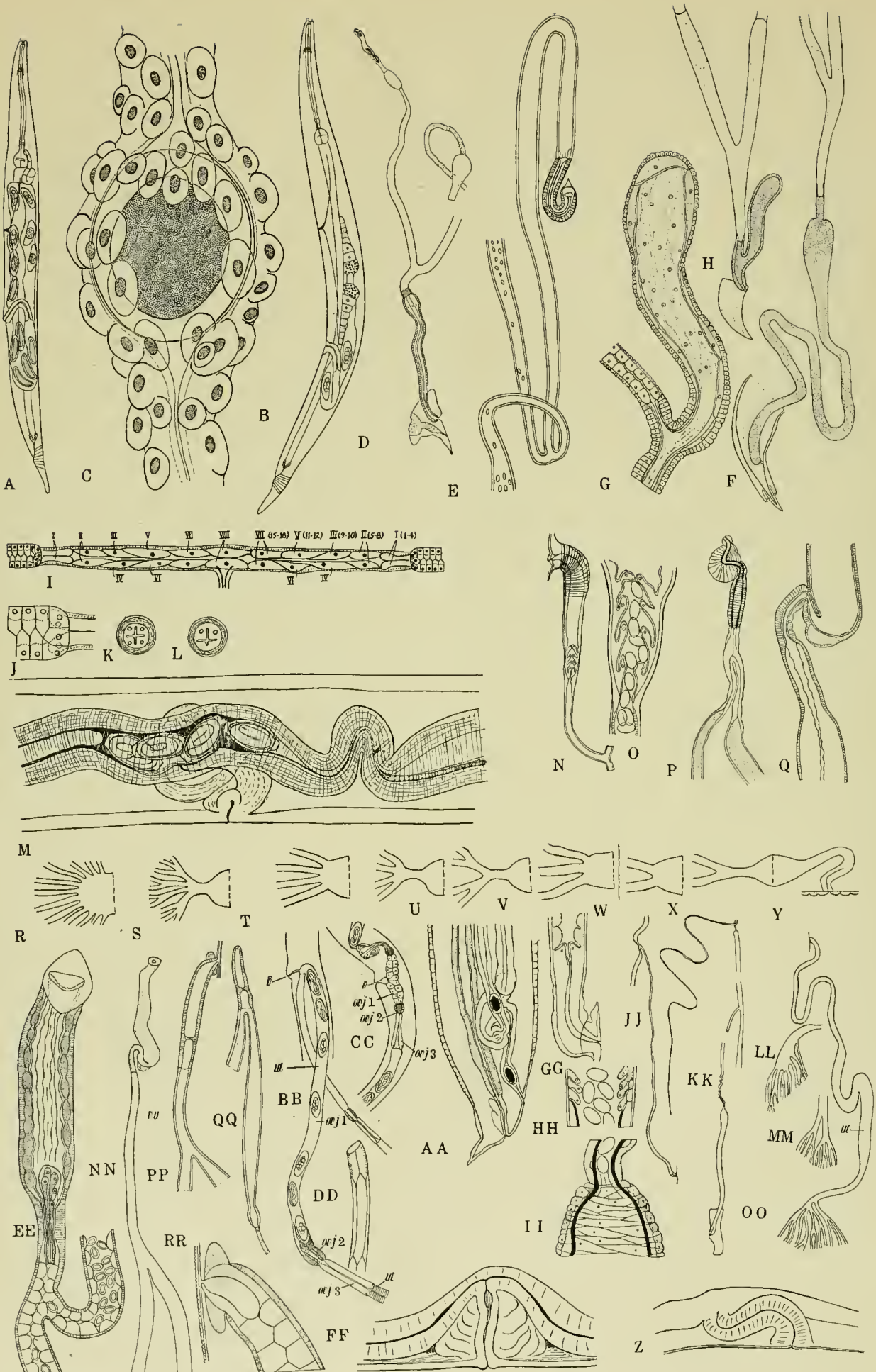
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Fig. 118.

In addition to the ordinary vaginal muscles there may be a large sphincter muscle at or near the vulvar opening; such a muscle (Fig. 122 B) is present in *Spironoura* and consists of one large muscle cell whose fibers are on its external surface. A similar cell has been observed in some free-living nemas (*Chromadora* sp. and *Sabatieria hilarula* Figs. 120 B & E). Dilator muscles of the vulva have already been mentioned (p. 43). In most cases transverse or modified somatic musculature serves to dilate the vulva.

COMPARATIVE MORPHOLOGY

FREE-LIVING PHASMIDIANS. The female reproductive system exists in its most simplified condition in the Rhabditoidea. The vagina is always simple, more or less transverse to the body axis, flattened, without special musculature and the uteri are likewise unmodified. Amphidelphic reflexed genital tubes are the rule, but monodelphic forms are also common. Studies on this group include Maupas (1900) on *Rhabditis dolichura*, Krüger (1913) on *R. aspera* (*R. aberrans*), Schleip on *Rhabdias bufonis*, Goodey (1935) on *Brevibucca saprophaga*, Thorne (1937) on *Cephalobus persegnis* and Steiner (1937) on *Eucephalobus teres*. In amphidelphic forms the vulva is always more or less equatorial in position (about 40-65 percent) and oddly enough this position is retained in the characteristically monodelphic family Cephalobidae. The vulva is preanal in other monodelphic forms such as *Brevibucca saprophaga* (Fig. 117 C), *Rhabditis lambdiensis* and *Longibucca*. Apparently reduction from the amphidelphic to the monodelphic condition is a sporadic happening throughout the Nemata, and in many other groups, such as the Rhabditidae the number of ovaries has no bearing on the degree of relationship and in that particular instance is not even a sound generic character as may be readily ascertained by comparing the males of the various monodelphic rhabditids (*R. lambdiensis*, *R. monhystera*, *R. spiculigera*, *R. ocypodis*). Prior to its use as a generic character at least one correlated, preferably non-female, character might be found. In the case of the Cephalobidae there is adequate evidence in the way of stomatal and male characters to indicate that ovarial reduction is a general character.

The uteri are usually thin-walled, composed of a low squamous epithelium in gravid females, while in quite young females the lumen may be minute, the epithelium thick. Monodelphic forms have a distinct postuterine sac (Fig. 117 B) in the Cephalobidae but not always in other families. A distinct seminal receptacle or spermatheca may or may not be present. In *Rhabditis strongyloides* (Fig. 116 A) there is a pair of seminal receptacles near the vulva; in *Brevibucca* (Fig. 117 C) Goodey described a pair of uninucleate uterine glands. The distal end of the uterus functions as a seminal receptacle and fertilization chamber in most rhabditoids (Maupas, 1900, Krüger, 1913, Goodey, 1924) even though it is not ordinarily distinctly set apart. Thorne (1937) has described a well defined spermatheca at the ovarial end of the uterus in *Cephalobus persegnis* (Fig. 117 B).

Fig. 118. FEMALE REPRODUCTIVE SYSTEM.

A-B—*Tachygonetria vivipara* (viviparous and oviparous females). C—*Rhigonema infectum* (Distal region of uterus). D—*Tetrameres nouveli*. E—*Acuaria anthuris* (Vagina and uteri). F—*Tetrameres inermis* (Vagina and uteri). G-H—*T. fissispina* (Vagina and uteri showing "Bursa copulatrix" or seminal receptacle). I-L—*Ancylostoma duodenale* (I—Diagram of ovejectors; J—Uterine end of ovejector; K—Cross section at level of II; L—Cross section at level of III). M—*Pseudomermis vanderlindei* (Vaginal region). N-O—*Spirura gastrophila* (Ovejector). P—*Habronema microstoma* (Ovejector). Q—*Habronema muscae* (Ovejector). R—*Physaloptera turgida*. S—*P. capensis*. T—*P. tumefaciens*. U—*P. paradoxa*. V—*Abbreviata abbreviata*. W—*Physaloptera cebi*. X—*P. retusa*. (R-X—diagrammatic representations of vagina showing uterine branching). Z—*Hydromermis leptoposthia* (Vagina). AA—*Oesophagostomum brevicaudum*. BB—*Nematodirus mauritanicus*. CC-DD—*N. filicollis* (DD, enlarged part of ovj. 1). EE—*Protospirura numidica*. FF—*Mesomermis bursata* (Vagina). GG—*Gongylonema mucronatum* (Vagina) HH-II—*G. scutatum* (HH, Junction of vagina vera and vagina uterina; II, Junction of constricted and dilated parts of vagina uterina). JJ—*G. mucronatum* (Vagina). KK—*G. scutatum* (Vagina). LL, MM & OO—*Abbreviata poicilometra* (Variations in uterine origin). NN & PP-RR—*Spirocerca lupi* (NN, adult; PP-RR, fourth stage larva). A-B, D-H, BB-EE, GG-KK, NN and PP-RR after Seurat, 1920, Hist. Nat. Nem. Berberie; M, after Steiner, 1937, Skrjabin Jubilee; R-X, after Schulz, 1927, Samml. Helminth. Arb. Prof. K. I. Skrjabin gewidmet; Z-FF, after Steiner, 1929, Zool. Jahrb., Abt. Syst. v. 57; AA, after Schwartz and Alicata, 1930, J. Agric. Res. v. 40 (6); LL-MM & OO, after Sandground, 1936, Bull. Mus. Comp. Anat. Harvard, v. 79 (6). Remainder original.

The degree of development of the oviduct is seemingly without significance in the Rhabditoidea since the existence of such an organ in some forms may be dependent on the age of the specimen. Within the superfamily diversity extends from no oviduct in *Rhabditis lambdiensis* and *R. strongyloides* to a well defined tube in *Rhabdias sphaerocephala*.

Diversity of ovarial form in the Rhabditoidea is limited chiefly to length; the ovaries never become coiled or greatly elongated organs as often occurs in the more highly evolved parasitic groups. Maupas (1900) and Krüger (1913) have demonstrated that in *Rhabditis dolichura* and *R. aspera* v. *aberrans* the ovary produces a limited number of spermatozoa prior to the appearance of oocytes. This type of reproduction is termed syngonism (Cobb, 1916) and is seemingly widespread among free-living nemas. In the hermaphroditic *Rhabdias*, Schleip (1911) found the syngone to produce spermatozoa and ova alternately.

The Tylenchoidea exhibit the same fundamental simplicities in the reproductive system as do the Rhabditoidea, but in this group monodelphic forms are much more common and are generally placed in separate genera from the amphidelphic types. The gonoducts may be either outstretched (*Ditylenchus dipsaci* Fig. 117 K) or flexed (*Anguina tritici*) or doubly flexed (*Hexatylus intermedius*.). This group also contains the only prodelphic didelphic free-living nemas, the highly specialized root parasites of the genus *Heterodera* (Fig. 117 P) and in members of the genus *Heterodera* the genital primordium is originally equatorial as in other nemas. Some of the oddities (ex. *Sphaerularia*, *Allantonema*) of the arthropod parasites comprising the Allantonematidae have been previously mentioned. Zur Strassen (1892), Leuckart (1887), Goodey (1930) and Bovien (1932) have made careful studies of the reproductive systems of *Bradynema*, *Allantonema*, *Sphaerularia*, *Tripius*, *Tylenchinema* and *Scatonema* (Figs. 115 A-B, E & I-K). In all instances the reproductive system is highly developed, and often the ovary becomes coiled and the uterus enormous. Unlike most parasites, these forms do not develop specialized mechanisms for the ejection of eggs but instead there is often degeneration and sometimes atrophy of the vulva and vagina.

FREE-LIVING APHASMIDIANS. Since most modifications of the reproductive system are related to increase in egg production and are associated with life habits rather than relationships, it seems best to cover the remainder of the free-living nemas before proceeding to the parasites. As previously noted, Filipjev (1918, 1934) has attached a great deal of weight to the position of the uteri and ovaries. It is true that in certain large groups the female genital tubes tend to be extended while in most nemas there is a flexure at the junction of ovary and oviduct regions in the gonoduct which caused it to be described as reflexed. Filipjev (1928, 1934) separated the Monhysterata, (equivalent to our Monhysteroidea and Axonolaimoidea and Microlaimidae) from the Chromadorata (equivalent to our Chromadoroidea, Desmodoroidea, and Plectoidea) on this basis, the female genital tubes being outstretched in the former group while they are "reflexed", or more properly speaking, *flexed* in the latter group. In so far as this is a tendency which is correlated with other characters, we recognize the soundness of its use as a taxonomic character. However, it must be stated that there is nothing so very fundamental in the differences, and other characteristics must also be considered. In addition, separations on the basis of the female reproductive system are not absolute since undeniable exceptions to the rule are known. Thus, the Comesomatidae, which otherwise show so many characters in common with the Axonolaimidae (Monhysterina) on the one side and with the Cyatholaimidae (Chromadorina) on the other side, present embarrassing exceptions. The genera *Dorylaimopsis* and *Laimella* with outstretched gonads must be ranged next to *Mesonchium* with flexed gonads, and *Comesoma minimum* has an anterior flexed and posterior outstretched gonad, while other members of the genus *Comesoma* supposedly have two outstretched gonads. Also, in the Microlaimidae (Chromadoroidea), *Microlaimus* and *Bolbolaimus* with outstretched gonads must be ranged next to *Achromadora*, *Ethmolaimus*, *Prodesmodora*, and *Statenia* with flexed gonads. *Halanonchus* (Fig. 117 N) is an example of a monhysterid with a flexed gonad. Similarly, the tendency of the members of the subfamilies Monhysterinae and


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Fig. 119.

Sphaerolaiminae to exhibit ovarial reduction is well recognized but no one would today exclude amphidelphic genera from these groups providing other characters conformed. In all nemic groups one notes the appearance of monodelphy and among free-living nemas, as also among parasites, this usually means posterior shifting of the vulva because it is the anterior ovary that persists. Exceptions to this rule are *Halanonchus macramphidium* (Monhysteridae), *Oxystomina cylindraticauda* (Enoplidae), *Dorylaimus monhystera* (Dorylaimidae) in all of which the vulva is shifted anteriad, the posterior ovary having persisted. In parasites, exceptions (Trichuroidea, *Dioctophyma, Soboliphyme*) to the rule seem to be as numerous as conformists but here there is probably some functional or fundamental reason as yet not understood.

If there is any single characteristic which might serve to contrast free-living aphasmidians with free-living phasmidians in the female reproductive system, it is a tendency toward the formation of larger, fewer eggs, often accompanied by marked relative shortening of the growth zone. The very large size of one or two maturing oogonia may give cause for a noticeable attenuation of the ovary, (Fig. 119 F). There are exceptional aphasmidians which produce numerous relatively small eggs (*Metoncholaimus pristiurus, Actinolaimus* sp. Fig. 120 G-H) and in such forms the ovaries are much more elongated, due to a more extensive growth zone.

The semi-diagrammatic illustrations speak largely for themselves. We need only call attention to the apparent absence of an oviduct in *Chromadora* (Fig. 120 E) and *Theristus* (Fig. 117 R), the individual and distinct oviduct of *Anaplectus, Axonolaimus, Sabatieria,* etc. and the modified oviducts of *Mononchus, Trilobus,* and *Actinolaimus*. In the latter forms there is marked flattening of the oviduct against the ovary (Fig. 120 H) and eventually the oviduct disappears as an entity, the ovarial epithelium being separated from the germ cells on one side so that the mature ovum may slip between the germ cells and the epithelium. This feature was first called attention to by Jägerskiöld (1901). The varied modifications serving the function of seminal receptacle or spermatheca are interesting from the standpoint that they may usually be regarded as the ovarial end of the uterus. Uterine outpocketing or separation from the oviduct in axonolaims and comesomes (Figs. 116 L-N) is sufficiently spectacular to lend considerable weight to hypothesized comesomatid-axonolaimid relationships.

Vaginal cuticle and muscular developments in free-living aphasmidians are often quite characteristic of species and genera but are, unfortunately, not easy to describe. Laminated vaginal musculature occurs very rarely, and in the genus *Trilobus* (Fig. 120 J) it is used as a specific character, being absent in many species. Often the vaginal cuticle appears in optical section of totomounts as two paired sclerotized rods (Fig. 119 I). Mononchs and dorylaims are particularly notable in this respect.

There is a very peculiar system of organs connected with the female reproductive system of oncholaimids first described by de Man (1886) and later studied by zur Strassen (1894) and Cobb (1930) and named the demanian system by Cobb. In description we can not do better than quote Cobb.

"*Demanian Vessels*: In adult female nemas (Oncholaims) a complicated double system of efferent tubes; connecting (1), with the middle or posterior part of the intestine through an *osmosium*, and (2), with the uterus (or uteri); these two efferents being confluent at a special glandular 'gateway', the *uvette*, and emptying thence backward and outward, through one or two ducts having more or less moniliform affluent glands. Normally, the ducts lead to exit pores in the body wall, usually lateral, one or more on each side, near the base of the tail." Cobb decided, on the basis of a systematic exploration of the theoretic possibilities, that the course of flow in the demanian system is from the intestine and uterus, through the moniliform glands to the exterior. Cobb associated this system with the formation of a "gelatin like" mass in the uterine lumen of gravid females which he believed flows out through the posterior pores and is deposited as a "sticky, non-water-soluble, nearly colorless secretion possibly utilized during agglomeration and copulation and also presumably to preserve the batches of eggs after deposition and segmentation." The writers (1938) observed orange pigmentation in the demanian exit ducts of *Oncholaimus oxyuris* which was similar to that found in the olivaceous sphaeroids of the same species.

Fig. 119. FEMALE REPRODUCTIVE SYSTEM.

A-C—*Spironoura affine* (A, showing posterior uterine branch. B, anterior branch; C, entire female). D—*Rhigonema infectum*. E, *Aphelenchoides fragariae* (Chrysanthemum strain). F—*Cryptonchus nudus*. G, *Halanonchus macramphidum*. H—*Ditylenchus dipsaci*. I, *Oxystomina cylindraticauda*.

A-C, after Mackin, 1936, Ill. Biol. Monographs v. 14 (3). Remainder original.

PARASITIC NEMAS. Seurat recognized the fact that the female reproductive system increases in complexity with the degree of parasitism. He noted tendencies in this direction among rhabditoids (ex. *Rhabdias*) and tylenchoids (ex. *Sphaerularia*). There is everywhere a tendency toward increased egg production, increased length and coiling of ovary, oviduct and uteri, and formation of complicated muscular ovejectors, but each parasitic group seems to have followed its own course of development.

Strongylina. Members of the Strongylina have a basically equatorial or slightly post-equatorial vulva joined to amphidelphic flexed gonoducts by means of a short transverse vagina and paired opposed ovejectors. Such a condition is approximately realized in *Dictyocaulus filaria* (Fig. 116 Q) and *Haemonchus contortus* (Fig. 116 T). Critical studies of the female organs of strongylins is due to the investigations of Augstein (1894), Looss (1905), Maupas and Seurat (1912), and Seurat (1920). In addition Ransom (1911), Seurat (1915), Veglia (1916), Thapar (1925), and Alicata (1935) have made contributions.

Varied nomenclatures applied to the ovejectors of strongylins have already been mentioned. The vagina vera in this group is always a short, more or less transverse flattened tube. As noted by Looss, the ectodermal cuticle stops suddenly at the junction of vagina and ovejector (Fig. 118 I). Seurat (1920) was apparently under the impression that the entire ovejector was of ectodermal origin because it was lined with "cuticle". However, the character of this cuticle is quite different from that of the vagina vera and external body covering. According to the observations of Alicata (1935) the ovejectors are formed from the central part of the genital primordium in *Hyostrongylus rubidus* while the vagina is an ectodermal invagination. With Looss (1905) we regard the ovejectors of strongylins as of totally uterine origin. There seems to be no evidence of glandular activity in any part of the ovejector so the term glazing (or varnishing) gland (see p. 147) is a misnomer. Each ovejector is composed of two (Fig. 118 I) or three parts (Fig. 118 CC). Its function in *Ancylostoma duodenale* was described by Looss as follows:

"The function of the pars haustrix (infundibulum) is evident from its structure. The contraction of the spiral muscles causes it to shorten, its inner cavity at the same time widening. The decrease of pressure thus brought about cannot be compensated for from behind, this being prevented by the funnel-shaped ends of the most anterior cells (I). The diminution of pressure therefore tells on what lies in front, sucking in the egg located nearest the pars haustrix. This egg is prevented from being pushed back into the uterus by a contraction of the anterior circular musculature of the pars haustrix, which, during the enlargement, has been passively extended. So soon as the egg has passed the funnel made by cells I, its way out is unimpeded. The return of the spiral musculature of the pars haustrix to its normal condition drives it into the pars ejectrix and it is ejected by the successive contractions of the muscles of the knobs. In passing from one knob to another, the egg follows a zig-zag course, but cannot escape backward, being prevented from doing so by the prolongations of the epithelial cells directed backward. In this way the egg is forcibly propelled onward into the vagina; from this it may be ejected either by pressure of the eggs forced on behind it or through the action of the vulvar muscles."

In *Ancylostoma* and several other members of the Strongylina each ovejector consists of only two parts. The uterine end, which Looss termed the *pars haustrix* (Fig. 118 I) consists of two sets of four cells (1 and II). This part apparently corresponds to the two parts of the ovejector of *Nematodirus mauritanicus* (Fig. 118 BB) described by Maupas and Seurat (1912) as *trunk* and

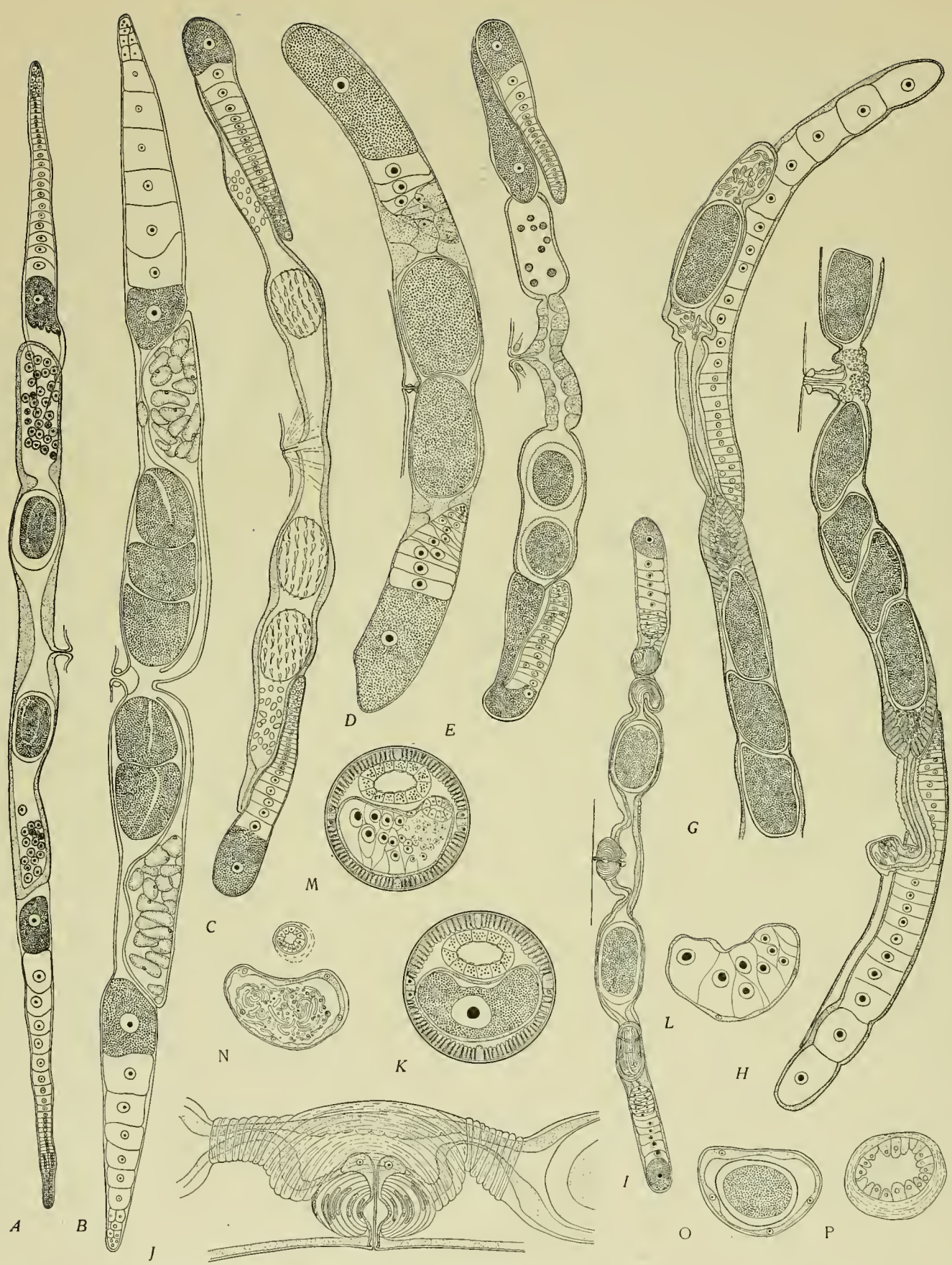

Fig. 120. FEMALE REPRODUCTIVE SYSTEM.

A—*Axonolaimus spinosus*. B—*Sabatieria hilarula*. C—*Anaplectus granulosus*. D—*Mononchus lacustris*. E—*Chromadora* sp., G-H—*Actinolaimus* sp. I-P—*Trilobus pellucidus* (I—female; J—Vaginal region; M—Germinal region of ovary; K—Distal or nearly ripe region of ovary; L — Growth zone; N — Seminal vesicle, with uterus above; O—Uterus in mid region; P—Uterus in vaginal region). Original.

sphincter (later renamed *sphincter* and *glazing gland*). Since, as Looss describes them, the four cells at the uterine end act as a suction funnel, we suggest the name *infundibulum* for them; and since the second group of cells act as a sphincter, the name is retained. The proximal part of each ovejector in *Ancylostoma* consists of four sets of two cells (III-VI) and one set of four cells (VII), making a total of 12 cells; in addition the two vaginal ends of the ovejectors are united with each other and with the vagina by four cells. For the uterine ends of the ovejector Looss' term *ejectrix* is retained. From the observations by Looss, Maupas and Seurat, and the writers examinations of *Oesophagostomum dentatum* and *Kalicephalus* sp., we judge cell constancy to be the rule for ovejectors in the Strongylina. The paired ovejectors with the union piece in *Ancylostoma* include 28 cells, the two sphincters and the two infundibula, four each or 16 cells making a total of 44. Seurat lists the ejectors as including 32, the sphincters two each, and the infundibula four each, also making a total of 44. We have found the same total in both nemas studied by us. Differences in appearance as suggested by Seurat are minor modifications; he found the same cellular arrangement in *Nematodirus mauritanicus* and *N. filicollis* but tremendous cellular hypertrophy in the ejector of the latter species. Slight modifications of cellular arrangement do exist, however, for we found tetraradiate symmetry (Fig. 122 P) throughout the ovejectors of *Ocsophagostomum* while Looss found sets of two cells in the ejectrix of *Ancylostoma* and Seurat a set of two cells in the sphincters of *Nematodirus*.

In no instance have the cells of the vagina vera been identified separately from the ectodermal epithelium. The musculature of the ovejectors is the same as the type which covers the uterus of nemas, that is, circular, oblique, and having spiral anastomosing fibers. When concentrated in a specific area they form a conspicuous sphincter.

The primary amphidelphic form is preserved chiefly in the families Ancylostomatidae and Trichostrongylidae (Fig. 116 T) in which the vulva tends to be only a short distance postequatorial. In the majority of other families of the suborder Strongylina the vulva is preanal in position. In such cases the paired ovejectors may separate in an amphidelphic manner before extending anteriad and thus becoming prodelphic as in *Oesophagostomum* or they may originate in a prodelphic manner as in *Kiluluma* (Fig. 117 X) and *Zoniolaimus* (Fig. 117 U).

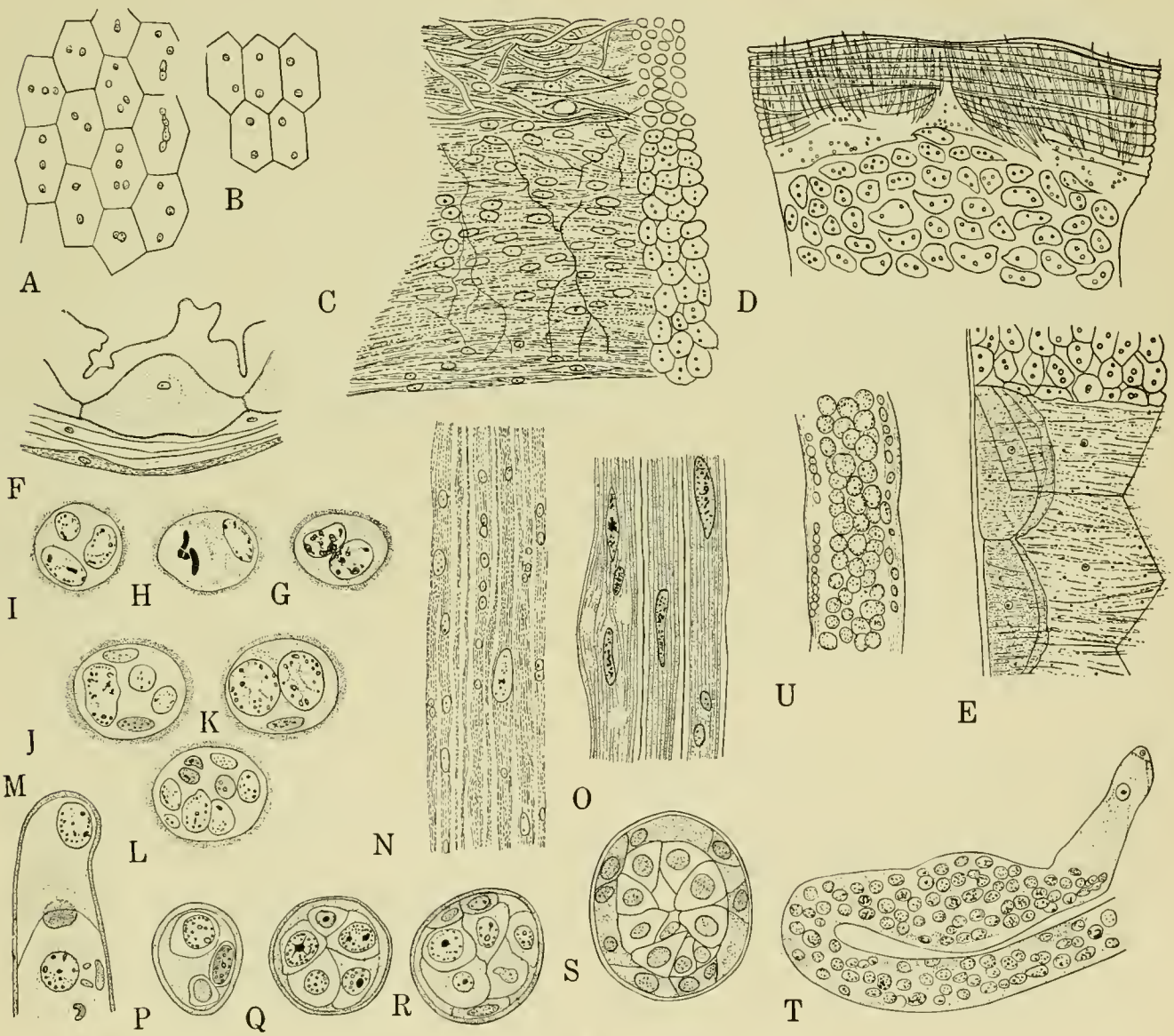

Fig. 121. *ASCARIS LUMBRICOIDES* SECTIONS.

A-B—Surface view of uterine epithelial cells. C—Junction of seminal vesicle and uterus. D—Junction of furrowed and smooth regions of oviduct. E—Junction of vagina uterina and vagina vera. F—Cross section of vagina vera. G-L—Cross sections of germinal region of testis. M—Surface view of blind end of testis. N—Surface view of epithelium in growth zone of ovary. O—Same near end of growth zone; P-S—Cross sections in germinal region of ovary. T—Totomount preparation of terminal region of ovary. U—Longitudinal section through germinal region of ovary. All after Musso, 1930, Ztschr. Wiss. Zool. v. 137 (2).

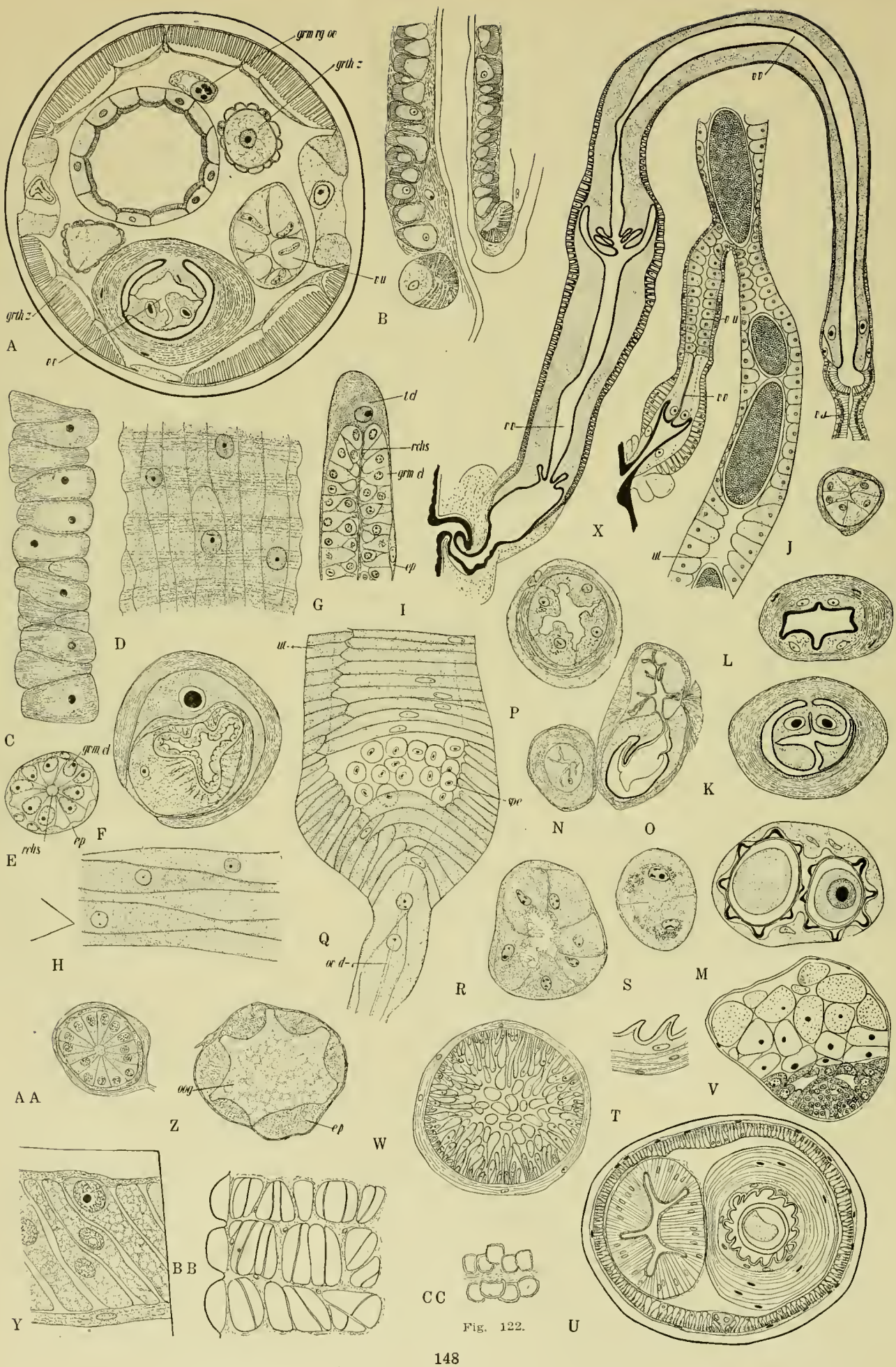
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Fig. 122.

When there is a reduction to one ovary as in heligmosomes (*Heligmosomum laeve*) there is a single ovejector having parts identical with the paired structure (Fig. 117 G).

The unspecialized sector of each uterus in *Oesophagostomum* consists of two rows of cells (Fig. 122 S) exhibiting possible glandular activity and a distinct bacillary layer. At its connection with the *infundibulum* the number of cells in a circumference is increased from two to six (Fig. 122 R). In practically all cases the ovaries are greatly elongated due to an extensive growth zone.

Ascaridina. Within the Ascaridina, vulva position varies from anterior to the base of the esophagus (*Protrellus künkeli*, Fig. 116 K) to practically anal (preanal in *Aorurus agile*, actually into the rectum in *Rondonia rondoni* 108 L). As in the Strongylina, there is usually a well-developed, muscular ovejector, particularly in the Oxyuroidea. The vagina vera is always elongated, usually tubular in the Oxyuroidea; and with the unpaired vagina uterina composes the ovejector. The internal structure of the vagina vera has been described (p. 141).

For all the marked specialization in ovejector formation, the superfamily Oxyuroidea contains some representatives which closely approach the free-living nemas. In practically all parasitic nemas the ovaries are filiform with an elongated growth zone. This is true of the majority of oxyuroids and ascaroids as well, but in the families Atractidae and Oxyuridae there are several examples with short tapering ovaries, and these forms, but for the vagina, might easily be mistaken for rhabditoids. *Tachygonetria vivipara* (Pharyngodoninae) typifies the amphidelphic organization while *Heth juli* (Ransomnematinae) typifies the prodelphic, didelphic, and *Labidurus gulosa* (Labidurinae) and *Atractis dactyluris* the prodelphic, monodelphic condition. Among the oxyurids vulvar position is extremely variable and the uteri are often parallel. In *Dermatoxys veligera* (Fig. 117 W), *Oxyuris equi* (Fig. 117 V) and *Syphacia obvelata* the vulva is shifted anteriad while the greatly elongated vagina uterina connects at the posterior end with the anteriorly directed uteri. Seurat (1920) interpreted this formation as modified prodelphy but Vogel (1925) has shown that on the basis of young specimens (Fig. 159 K), *Syphacia* and *Dermatoxys* must be considered primarily *amphidelphic* like *Tachygonetria vivipara*. Similarly *Protrellus känckeli* is an amphidelphic thelostomatid example of vulvar shifting, with elongation of vagina uterina; *Cephalobellus papilliger* and *Hystrignathus rigidus* exemplify the standard condition. A well marked vagina uterina (ovejector) is characteristic of all thelastomatids and oxyurids but not of atractids. The Rhigonematidae are a group apart, in the Oxyuroidea, in female structures as in other characters. They are more like the Ascaridoidea in that only the vagina vera takes part in the formation of the heavily walled ovejector. In *Rhigonema infectum* (Fig. 119 D) the vagina vera is connected with a massive sac and through this with the amphidelphic uteri. Artigas (1930) found this chamber absent in other species and formed for them a new genus, *Dudekemia*. In *R. infectum* the ovarial end of each uterus is set apart and serves as a spermatheca and fertilization chamber; we therefore presume the larger chamber to be an egg pouch.

Fig. 122. FEMALE REPRODUCTIVE SYSTEM.

A-H—*Spironoura affine* (A—Cross section near vulva; B—B—Longitudinal section of vagina; C—Surface section of vagina showing muscles; D—Surface view of uterus showing epithelium and muscles; E—Cross section of germinal region of ovary; F—Cross section of vagina; G—Longitudinal section of blind end of ovary; H—Surface view of epithelium in growth zone of ovary). I—*Macracis monhystera* (Longitudinal reconstruction of vagina vera). J-M and X—*Hystrignathus rigidus* (J—Cross section of vagina uterina; K-L—Cross sections of vagina vera, K at valve; M—Uterus; X—Longitudinal reconstruction of vagina and uteri). N-S—*Oesophagostomum dentatum* (N-O—Adjoining parts of ovejector, N is uterine while O shows connection of vagina vera to other ovejector; P—Distal part of ovejector; R—Uterus near ovejector; S—Uterus more distal). T-U—*Trichuris ovis* (T—detail of vaginal cuticle; U—Cross section near vulva). V—*Trichuris suis* (Ovary showing germinal region on one side). W—*Dioctophyma renale* (Ovary showing germinal zone extending around surface). Y-AA—*Cephalobellus papilliger* (AA—Ovary in germinal zone; Y and Z—Ovary in growth zone). BB-CC—*Enterobius vermicularis* (Uterine musculature in living specimens, BB relaxed and CC contracted).

V, after Rauther, 1918, Zool. Jahrb. Abt. Morph. v. 40; W, after Rauther, 1930, Handb. Zool. v. 2; Y-AA, after Chitwood & Chitwood, 1933, Ztschr. Zellforsch. v. 19 (2). Remainder original.

Within the Ascaridoidea no forms are known that approach the simplicity of *Tachygonetria vivipara*; the ovaries are always greatly elongated, commonly coiled. Within the Cosmocercidae, Kathlaniidae* and Heterakidae, most of the forms are primarily amphidelphic, with the vulva usually more or less equatorial, while the Ascarididae contain forms which are chiefly opisthodelphic, with vulva shifted anteriad. The ovejector is seldom as prominent an organ in this superfamily. In so far as information is available the vagina of cosmocercids (Olsen, 1938) and kathlaniids (Mackin, 1936) is entirely vagina vera, i. e. the ectodermal part extends to the separation of the two uteri.

In *Heterakis gallinae* (Heterakidae) the heavily muscled ovejector (Fig. 116 R) is vagina vera but in addition there is an elongated vagina uterina which extends posteriorly and is reflexed anteriad before connecting with the amphidelphic uteri. For such a (relatively) non-muscular modification of the vagina uterina we feel that Seurat's term "trompe" or trunk may properly be reserved. This same term would apply in the case of *Rhigonema* (Fig. 119 D). Other heterakids including *Ascaridia lineata* (Ackert, 1931), *Allodapa numidica* (Seurat, 1915) and *Maupasina weissi*† (Seurat 1931) have a short ovejector composed of vagina vera and a long trunk composed of vagina uterina. The two former species are amphidelphic while the latter is prodelphic and like *Rhigonema*, possesses a large chamber at the end of the ovejector, Seurat named this structure a *bursa copulatrix* considering that it might function as a temporary storage place for spermatozoa. Such a structure also occurs in some spiruroids.

Ascaridids are opisthodelphic as represented by *Ascaris lumbricoides* (Fig. 117 L); the vulva is usually situated preequatorially, the vagina directed posteriad, followed by trunk and posteriorly directed parallel uteri. As in heterakids, the vagina uterina (trunk) is not conspicuously muscular and in many forms there is a dilation at its distal end which might serve equally well as a temporary spermatheca (*bursa copulatrix*) or as a temporary egg chamber. Polydelphy makes its appearance in the genus so named, *Polydelphis*, in which there are four parallel uteri arising at the end of the trunk while the twin genus *Hexametra* is identical except that there are six uteri.

Camallanina. In this suborder the reproductive system is chiefly amphidelphic, the vulva more or less equatorial. Within the Dracunculoidea, the vagina is never heavily muscled, nor are the uterine ovejectors developed. In *Philometra* and *Dracunculus* the vagina is functional only in young females, becoming rudimentary with gravidity; in *Micropleura* it is retained but not especially developed. The uteri of dracunculoids are great sacs dilated with embryos and larvae filling practically the entire body cavity. Camallanoids, on the contrary, retain a functional muscular ovejector formed by the vagina vera. In addition there may be a pair of short uterine ovejectors in *Cucullanus* (116 H) or an elongate tubular trunk in *Camallanus* (Fig. 117 H). The family Camallanidae is monodelphic, prodelphic but a postuterine sac is generally present. The family Cucullanidae, while developmentally amphidelphic, contains some transitions toward prodelphy.

Spirurina. In this suborder there is a well developed muscular ovejector, the very heavily muscled part of which is properly considered a vagina vera. Opisthodelphic, amphidelphic and prodelphic forms are all represented commonly within the group. Of these the opisthodelphic forms are chiefly to be found in the Filarioidea, Thelaziidae and Physalopteridae in all of which the vulva is predominantly anterior in position. However, even in these groups exceptional forms are amphidelphic (*Desmidocercella* Filarioidea), prodelphic (*Physocephalus*, Thelaziidae; *Proleptus*, Physalopteridae). The remaining families, Spiruridae, Acuariidae and Gnathostomatidae might be termed primarily amphidelphic or prodelphic but there is too much variation except in the Gnathostomatidae for any generalization. The vagina vera seldom if ever reaches the bifurcation of the uteri so that there is always a trunk. This trunk has high epithelial cells which extend to a variable degree beyond bifurcation of

*The structure termed "shell gland" by Mackin (1936) is the oviduct.

†The uteri are parallel and directed anteriad, thereafter reflexed posteriad, the ovaries being situated in the caudal region. Seurat (1920) characterized this formation as opisthodelphic.

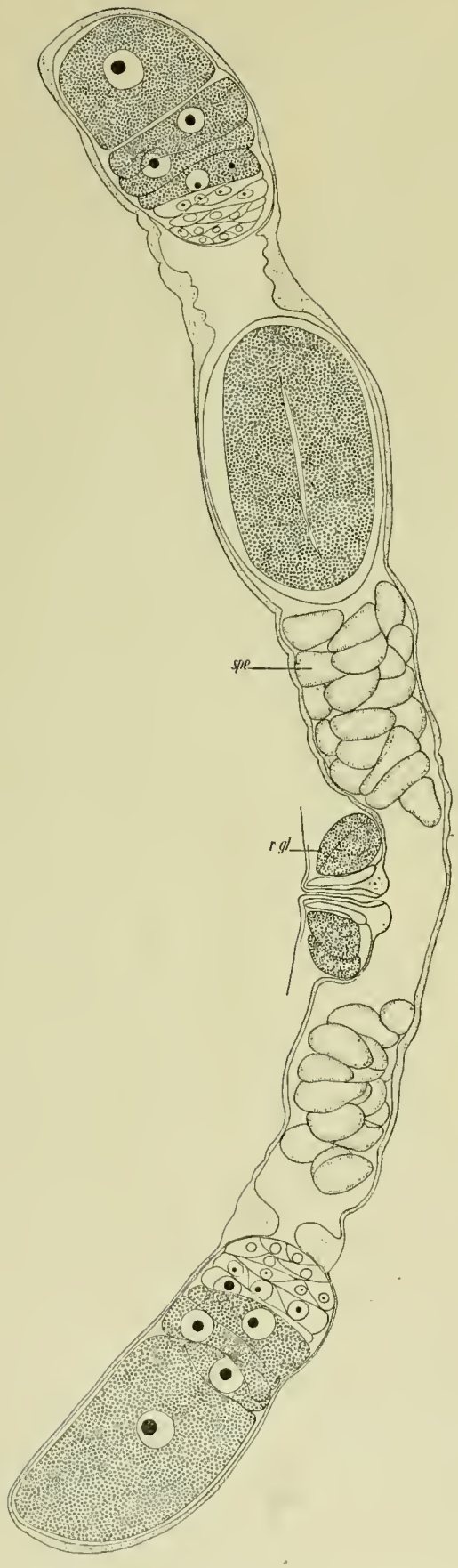

Fig. 123. FEMALE REPRODUCTIVE SYSTEM. *Halichoanolaimus robustus*. Original.

the uteri. The various arrangements have been studied by Seurat (1920) in *Acuaria laticeps, Tetrameres fissispina, Spirura gastrophila, Protospirura numidica* and *Abbreviata abbreviata* (Fig. 118). The Physalopteridae present more taxonomic difficulty than any other group because of their tendency toward polydelphy. Ortlepp (1922, 1937) divided the genus *Physaloptera* into four groups (Didelphys, Tridelphys, Tetradelphys and Polydelphys) on the basis of uterine and ovarial numbers. At the same time he attempted to follow out correlations according to the method of uterine origin, i. e., whether the uteri arose direct from the base of the egg chamber (trunk) (Fig. 118 X) or were connected to the egg chamber by a common trunk (Fig. 118 Y). In the didelphic, tetradelphic and polydelphic types the two possibilities both made their appearance. Schulz (1927) compared these data with cephalic characters and came to the conclusion that ovarial number must be considered a secondary character, and mode of origin of the uteri a tertiary character. Thus the old genus *Physaloptera* was divided into three genera on the basis of cephalic structures, each genus being subdivided on ovarial number. Apparently Sandground (1936) has substantiated Schulz in discarding mode of origin of the uteri as a character since he showed three modes of uterine origin in the species *Abbreviata poicilometra* (Fig. 118 LL-MM & OO).

Polydelphy outside the Physalopteridae is unusual, having been recorded only in *Elaeophora poeli* and *Tanqua tiara* (Fig. 116 U), Dipetalonematidae and Gnathostomatidae respectively. In the latter form one encounters polydelphy and amphidelphy associated, there being three anterior uteri and one posterior uterus all of which empty into a common egg chamber which is in turn connected with the vagina (Monnig, 1923).

Mermithoidea. The Mermithoidea are purposely taken up here, along with the vertebrate parasites because they exhibit the same characteristics of vaginal development as do the more generally considered forms. Steiner (1923, 1926, 1929) has described a remarkable series of stages in the formation of an elongate muscular vagina from the transverse slit characteristic of all dorylaims, as seen in *Mesomermis bursata* (Fig. 118 FF), enlargement as in *Bathymermis sphaerocephala* and elongation as in *Hydromermis leptoposthia* (Fig. 118 Z), to the complex type found in *Limnomermis cuvaginata*. As in many other parasitic groups, Steiner (1923) found that there is elongation of the oviduct. Mermithoids are always amphidelphic, so far as known.

Trichuroidea - Dioctophymatoidea (Hologonia). The specific details of differentiation of these two groups from other vertebrate parasitic groups rests not only on reproductive system, but on hypodermis, coelomocytes and stylet formation. Just how significant is the altered type of germ cell origin, upon which Rauther (1930) based the Hologonia, we are not prepared to say. All members of the group are monodelphic and in all with the exception of the genera *Eustronaylides* and *Hystrichis* the vulva is anteriorly shifted. The muscular ovejector so far as known is of ectodermal origin.

Male Reproductive System

GENERAL MORPHOLOGY

There has been no comparative morphological study on the male reproductive system comparable to that of Seurat on this system in the female. This is due, at least partially, to the structural uniformity of the male apparatus which lacks distinct adaptation coincident with parasitism; as in the female, with parasitism the male reproductive system increases in length but accessory structural differentiations are not apparent.

There may be either one or two testes. If two, they are arranged in opposite directions except in *Heterodera marioni* and *Anticoma typica*. In the first species there may be either one or two testes continuous posteriad with a single seminal vesicle; transitions apparently indicate that the double condition arises as a longitudinal split of a single original testis. This is quite different from the normal origin of double testes in which they grow apart as they form at the two poles of the genital primordium. *Heterodera marioni* is the only example with two testes known in the Phasmidia. In *Anticoma typica*, Cobb 1890, described a form with parallel testes in tandem. This arrangement (Fig. 124 L) may easily be considered as due to a shift of the posterior testis from a normally opposed to a tandem position.

Flexure of the testis is common in the Phasmidia (*Rhabditis*, Fig. 124 A) but just how widespread the phenomenon is we do not know. In *Heterodera marioni* the one or two testes may be either flexed or outstretched. In the Aphasmidia, flexure is unknown except in some of the forms with a single testis.

The same differentiation of groups according to origin of germ cells is seen in the male as in the female (p. 135); hologonic forms (*Dioctophymatoidea* and *Trichuroidea*) have an extended region of germ cell formation while in the remaining nemic groups germ cell formation is confined to the end of the testis.

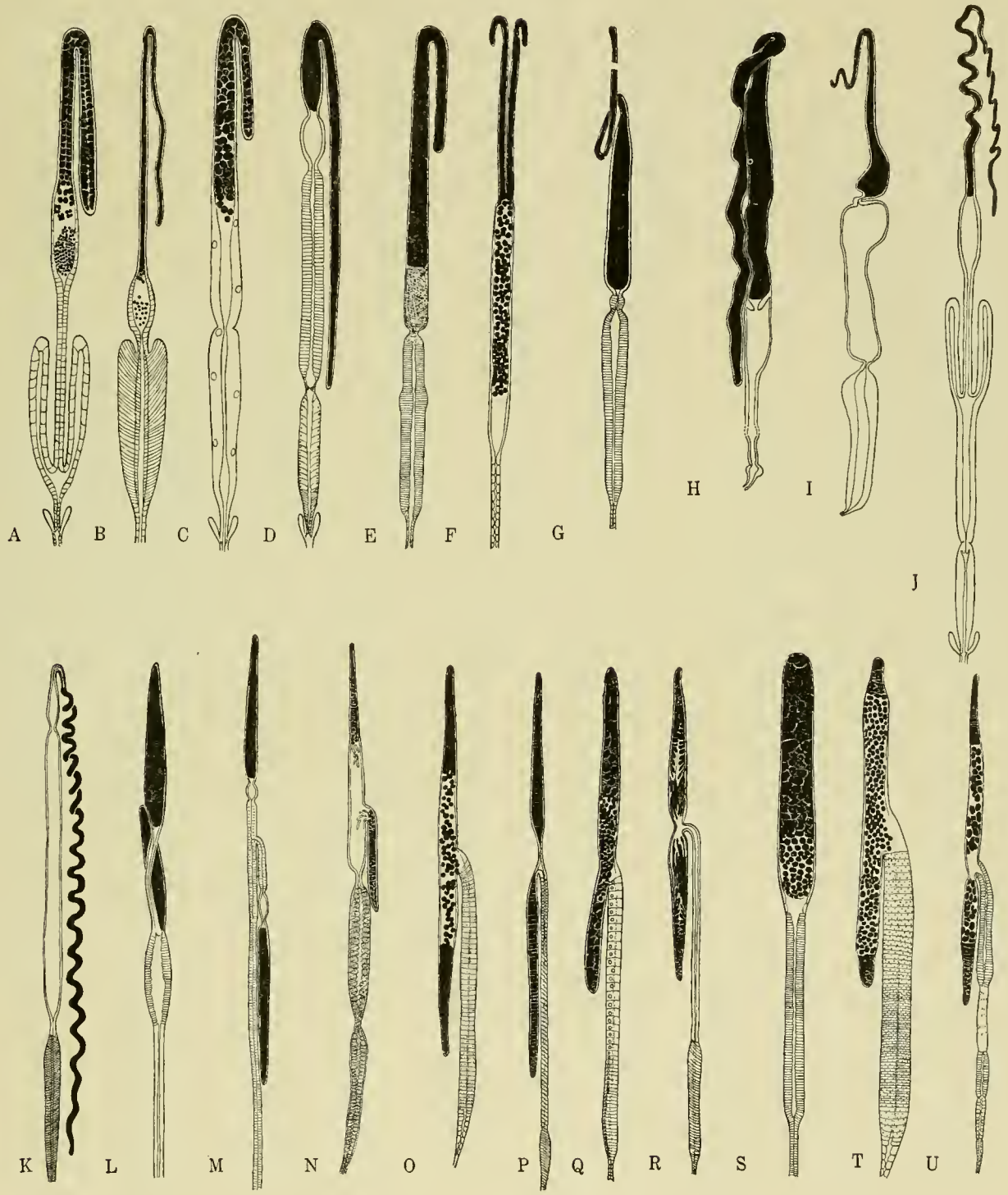

Fig. 124.

Diagrams of male reproductive system. The epithelial portions are white, the germinal portions black. When rectal (i. e. cloacal) glands are known to be attached to the ejaculatory duct (A, C, D) they are shown as lateral protuberances. A—*Rhabditis strongyloides*. B—*Oesophagostomum dentatum*. C—*Rhabditis lambdiensis*. D—*Spironoura affine*. E—*Rhigonema infectum*. F—*Heterodera marioni* (with two testes). G—*Heliconema anguillae*. H—*Cucullanus heterochrous*. I—*Camallanus lacustris*. J—*Heterakis gallinae*. K—*Trichuris suis*. L—*Anticoma typica*. M—*Agamermis decaudata*. N—*Enoplus communis*. O—*Desmolaimus zeelandicus*. P—*Metoncholaimus pristiurus*. Q—*Anaplectus granulosus*. R—*Trilobus gracilis*. S—*Chromadora quadrilinea*. T—*Halichoanolaimus robustus* (*Spilophorella paradoxa* and *Metachromadora onyxoides* are similar). U—*Sabatieria hilarula*. G, After Yamaguti, 1935, Jap. J. Zool. v. 6 (2). H & I, after Toernquist, 1931, Goeteborgs Kungl. Vetenskaps. o. Vitterhets-Samm. Handl. s. B, v. 2 (3). K, after Rauther, 1918, Zool. Jahrb. Abt. Anat. v. 40. L, after Cobb, 1890, Proc. Linn. Soc. N. S. Wales, s. 2, v. 5. M, after Steiner, 1923, J. Heredity, v. 14 (4). Remainder original.


A
v def
dct ej
B
gl
sem v
C
v def
dct ej
D
v def
E
F
G
sem v
v def
ntb
H
ntc
I
v def
J
dct ej
K
L
sem v
v def
M
v def
dct ej

Fig. 125.

Many phasmidian nemas have a rachis to which the spermatogonia are attached (*Ascaris*, *Spironoura*, *Heterakis*, the Strongylina in general and rhabditids). This structure is apparently a process from the cap cell or terminal epithelial cell of the testis similar to that of the ovary (p. 139).

Parts of the Male Reproductive System. The male reproductive system consists of three or four major divisions, the basic and more general divisions are testis, seminal vesicle and vas deferens (Fig. 3). In some of the more highly developed parasites such as *Ascaris lumbricoides* and *Trichuris suis* (syn. *T. crenatus*) a testicular duct, the *vas efferens* (Samenleiter) separates the testis from the seminal vesicle. The terminal (posterior) end of the vas deferens may be set off as an ejaculatory duct.

Testis. In telogonic nemas the testis is subdivisable into two regions, *germinal zone* and *growth zone*. In phasmidians the cells of the growth zone first take the form of a chord of six or more radiating series of cells attached centrally to the protoplasmic rachis while in aphasmidians they more often take the form of a four cell chord which rapidly gives place to a double row and finally a single chain of cells. In all cases except hologonic forms the testis is covered with an epithelium continuous with that of the seminal vesicle (or vas deferens) just as the ovary is covered with an epithelium continuous with that of the oviduct.

Vas efferens. In the few instances where such a structure has been described it is a duct separating the growth zone of the testis from the seminal vesicle. It has a rather high simple cuboidal to columnar epithelium.

Seminal vesicle. This is a dilated part of the male gonoduct which acts as a storage organ for sperms. The vas efferens may be considered as a specialized tubular part of this structure.

Vas deferens. The vas deferens is the chief part of the male gonoduct. It is generally subdivided into tubular and glandular regions and it may be covered by a muscular layer either in its terminal region (near the cloaca) or throughout its length. Thus only a part of the structure is usually the functional ejector or ejaculatory duct. The detailed anatomy of the vas deferens changes so much in the various groups that it will be considered with the description of special anatomy.

COMPARATIVE MORPHOLOGY

As previously discussed the Phasmidia characteristically have a single testis. Among the aphasmidians the Trichuroidea and Dioctophymatoidea also have a single testis. No comprehensive surveys have been made which would permit unequivocal characterizations of other groups but two testes are the typical condition, so far as known, of the remaining aphasmidian groups.

Marked development of musculature covering the ejaculatory duct does not parallel parasitism as does marked development of this layer in the female gonoduct. On the contrary, it is very markedly correlated with the taxonomic group. So far as known, a heavily and extensively muscled ejaculatory duct occurs only in the order Enoplida and holds true as a taxonomic character in all its representatives studied by the writers. This is particularly interesting since it so clearly confirms the placement of the Trichuroidea and Dioctophymatoidea in this order.

Phasmidia. The male reproductive system of this group has been studied by Schneider (1866) on *Rhabditis strongyloides*, by Leuckart (1876) on *Ascaris lumbricoides*, by Cobb (1888) on *Anisakis*, by Looss (1905) on *Ancylostoma*, by Jägerskiöld (1909) on *Dichelyne*, by Krüger (1913) on *Rhabditis aspera* (*R. aberrans*), by Magath (1919) on *Camallanus*, by Steiner (1923) on *Agamermis decaudata*, by Musso (1930) on *Ascaris*, by Chitwood (1930) on *Rhabditis*, by Törnquist (1931) on *Camallanus* and *Cucullanus*, by Chitwood (1931) on *Oesophagostomum*, by Chitwood & Chitwood (1933) on *Cephalobellus*, by Yamaguti (1935) on *Heliconema*, by Baker (1936) on *Heterakis* and by Mackin (1936) on *Spironoura*. Other workers have made more or less casual observations incidental to studies of spermatogenesis or postembryonic development.

The chief point of interest is the diversity in structure of the vas deferens. At its junction with the seminal vesicle there may be a well marked constriction. The duct may be incompletely differentiated into an anterior glandular region, comprising the greater part of its length and a posterior non-glandular region or ejaculatory duct, as in *Rhabditis lambdiensis*, *Cephalobellus papilliger* and *Heliconema anguillae*. (Figs. 124 C & G). In others the anterior part may be subdivided into two sections both of which may be glandular but the form of the epithelium and the character of the secretory masses differ in the two regions; this occurs in *Rhigonema infecta* and *Spironoura* spp. (Fig. 124 D & E). In the latter forms there is a distinct valve between anterior and posterior sections. A similar division has also been noted in *Cucullanus*, *Camallanus* and *Ascaris*. At the division point there is a muscular sphincter in many forms. Musso and Magath claimed to have seen at least one nucleus in the sphincter but other authors have been unable to observe such. Muscular fibers in general are always very sparse and confined to the second and third (or just the third) zone of the ejaculatory duct. As first pointed out by Voltzenlogel (1902) they appear to originate with the posterior intestinal muscles and are without nuclei of their own.

A second general type in the Phasmidia is exemplified by *Rhabditis strongyloides* (Fig. 124 A). In this form the vas deferens has two large lateral pouches which extend anteriorly on both sides. Here there has been a differentiation of purely epithelial cells (forming the anterior section of the vas deferens) and glandular cells (forming the pouches and mid-section of the duct). These pouches were first described by Schneider and later studied by Chitwood (1930); they are called ejaculatory glands and are thought to form the adhesive cement deposited on the female at copulation. They seem to have arisen as a minor modification of the glandular region generally typical of phasmidian forms. Looss has described very similar though incompletely separated ejaculatory glands in *Ancylostoma* and the writers have seen such in *Oesophagostomum*. In the latter form the glandular cells are often so placed as to give a laminated appearance (Fig. 124 B) and purely epithelial cells are distinctly recognizable along the dorsal side of the vas deferens in the glandular region. Chitwood (1931) described processes from these cells which he considered possible homologues of cilia; Cobb (1888) and Rauther (1918) had previously described hair-like processes from the epithelial cells of the vas deferens of ascaridids and trichuroids respectively. None of these authors have observed vibratile movements. In *Heterakis* Baker found ejaculatory glands very similar in gross morphology to those of *Rhabditis strongyloides* but in this form there are four distinct sections of the vas deferens (Fig. 124 J). These sections consist of a narrow tubular anterior part continuous with the seminal vesicle, two wider glandular sections, separated from one another by a valve, and a short posterior ejaculatory part. In this case the paired ejaculatory glands open into the anterior end of the first glandular section. Whether they should be interpreted as outpocketings of that part or as differentiated lateral outpocketings of the tubular anterior section, is not known.

Aphasmidia. Study has been made of the male reproductive system of members of this group by Eberth (1860) on *Trichuris*, by Leuckart (1876) on *Trichuris*, by de Man (1886) on *Enoplus*, *Anticoma*, *Tripyloides* and *Euchromadora*, by Cobb (1890) on *Anticoma*, by Jägerskiöld (1901) on *Cylicolaimus*, by Türk (1903) on *Thoracostoma*, by Schepotieff (1908) on *Desmoscolex*, *Greeffiella* and *Epsilonema*, by Rauther (1918) on *Trichuris*, by Steiner (1923) on *Agamermis*, by Cobb (1928) on *Spirina* and by Cobb (1929) on *Draconema*. In addition to these papers numerous authors have noted the number of testes in descriptions of species. Cobb, however, is the only author who consistently provided such information.

As previously noted above, the two aphasmidian orders, so far as existing information goes, may be separated upon the basis of muscular development of the ejaculatory duct.

Fig. 125.

Male reproductive system. A—*Rhabditis lambdiensis*. B-C & F—*Heterakis gallinae*. (B—Anterior part of gonoduct; C—Posterior part of gonoduct; F—Cross section at level of ejaculatory glands and vas deferens). D-E—*Chromadora quadrilinea* (D—Testis and upper part of vas deferens; E—Spermatozoan). G-H—*Spironoura affine*. (G—Totomount male; H—Detail of valve indicated by *vlv* in G). I-J—*Sabatieria hilarula*. (I—Anterior part of gonoduct; J—Posterior part of gonoduct). K-L—*Heterodera marioni* (Monorchic form; K—Anterior part of gonoduct; L—Posterior part of gonoduct). M—*Trilobus gracilis*. G, After Mackin, 1936, Ill. Biol. Monogr., v. 14 (3). Remainder original.

Within the Order Chromadorida the ejaculatory duct has very little musculature, and that is discernible only under the most favorable conditions. From this standpoint, members of the group are definitely closer to phasmidians such as *Rhabditis* than are members of the other aphasmidian group, the Enoplida. Diorchic* forms are the rule but *Euchromadora, Chromadora Monoposthia, Spirina, Epsilonema, Tripyloides, Desmoscolex* and *Greeffiela* are all monorchic. According to Cobb, some species of *Monhystera* and *Cyatholaimus* are monorchic. Examples of forms known to be diorchic include *Anaplectus granulosus, Aphanolaimus* spp., *Bastiania exilis*, axonolaimids, comesomatids, cyatholaimids, *Spilophorella paradoxa, Desmolaimus zeelandicus, Theristus sctosus* and *Draconema cephalatum*. Flexure of the gonoduct is limited to some forms with one testis (*Anaplectus granulosus* sometimes exceptional).

The typical testicular arrangement (Fig. 124 O) consists of two testes extending in opposite directions but joined by a pair of seminal vesicles which may or may not be clearly separated from one another by a constric-

*Monorchic (with one testis) and *diorchic* (with two testes) are here introduced as adjectives comparable to monodelphic and didelphic which are used to denote the number of ovaries.

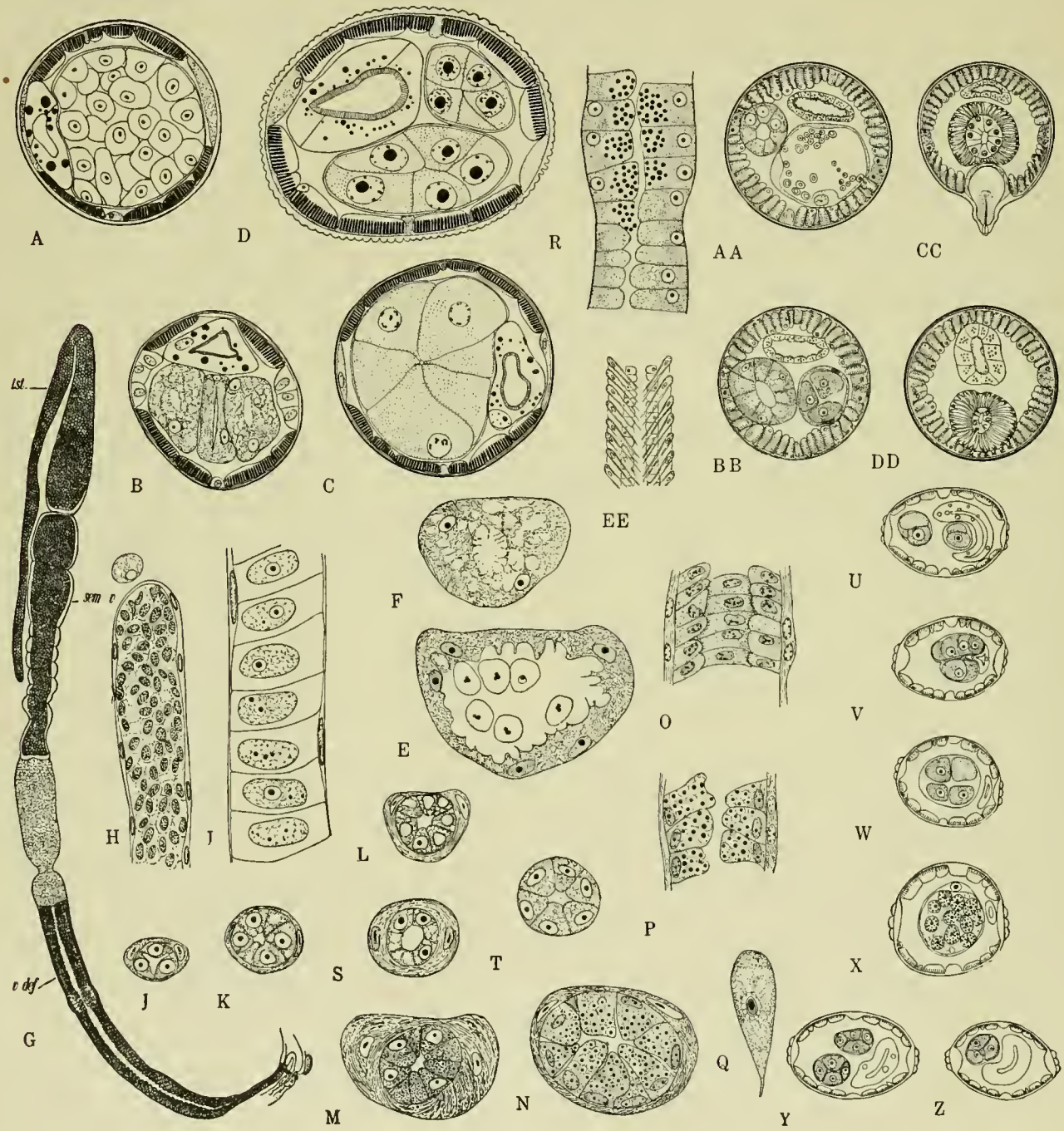

Fig. 126.

A-C—*Rhabditis terricola*. (A—Cross section at level of seminal vesicle; B—Vas deferens with ejaculatory glands on each side; C—Testis just anterior to seminal vesicle). D-F—*Rhabditis lambdiensis* (D—At level of testis; E—Seminal vesicle; F—Vas deferens). G—*Rhigonema infectum* (male gonoduct). H-K & S-T—*Metoncholaimus pristiurus* (H—Blind end of testis; I—Growth zone of testis; J—Ejaculatory duct just preanal; K—Vas deferens; S—Ejaculatory duct mid-region; T—Vas deferens opposite seminal vesicle). L-Q—*Enoplus communis* (L—Ejaculatory duct just preanal; M — Ejaculatory duct mid-region; N—Vas deferens; O—Ejaculatory duct; P—Glandular region vas deferens; Q—Sperm). R—*Chromadora quadrilinea* (Junction of glandular and non-glandular regions of vas deferens). U-Z—*Heterodera marioni* (U-Y—Diorchic specimen; Sections at intervals from anterior, posteriad in the order Y, U, V, W, X, [X—Seminal vesicle]; Z—Specimen monorchic). AA-EE—*Trilobus gracilis* (AA—Showing vas deferens and seminal vesicle; BB—Vas deferens and testis; CC—Mid-region of ejaculatory duct; EE—Longitudinal section of ejaculatory duct). Original.

tion. At the junction of the seminal vesicles, the vas deferens is given off as a single tubular canal directed posteriad. This structure is highly glandular throughout its length. Rarely (*Sabatieria*) the posterior part may be set off by a constriction (Fig. 124 U). A very short non-glandular terminal division acts as ejaculatory duct. In monorchic forms (*Chromadora*) the arrangement (Fig. 124 S) is so similar to that of *Rhabditis lambdiensis* that it needs no special description. De Man mentioned special copulatory glands in *Euchromadora* and Schepotieff did the same for *Desmoscolex* but in neither instance is an adequate description or illustration furnished.

Three types of spermatozoa are known in the Chromadorida, these being standard ameboid (typical of the Phasmidia), flagellate, and hollow. Of these, the flagellate type of spermatozoan is known only in *Halanonchus* and the ameboid is known in plectids, chromadorids and *Desmolaimus*. The hollow sperm is a very interesting and peculiar structure. As a rule it is large with a narrow ectoplasm radially striated by fibrils and a central vacuole. The nucleus usually lies next to the periphery and is quite small (exception *Spirina parasitifera*). This type of sperm is known to occur in axonolaimids, comesomatids, cyatholaimids, *Tripyloides*, *Microlaimus*, *Monoposthia* and *Metachromadora*.

Within the Order Enoplida the musculature of the ejaculatory duct is usually very prominent and may extend to the seminal vesicle. So far as known, all Enoplida are diorchic except the hologonic groups Trichuroidea and Dioctophymatoidea. In these the musculature of the ejaculatory duct is particularly thick, giving a laminated appearance due to the presence of several layers of muscle cells. Steiner (1923) has shown the entire vas deferens of *Agamermis decaudata* as being covered by a well developed muscular layer. The writers have found the ejaculatory duct covered by a particularly well developed layer of oblique muscles in *Metoncholaimus* (Fig. 126 S) *Trilobus* (Fig. 126 DD-EE), *Enoplus* (Fig. 126 L-N), and *Phanodermopsis*; the muscle cells in these forms extend only half way around the ejaculatory duct, extending obliquely anteriad from the medio-ventral to the medio-dorsal line. In *Metoncholaimus* the musculature extends anteriad, in a less well developed manner for over half the length of the vas deferens while in *Enoplus* the musculature extends throughout the length. Glandular activity is evident throughout the vas deferens and the anterior part of the ejaculatory duct in *Enoplus* while it is confined to the vas deferens in *Trilobus*, *Thoracostoma* and *Cylicolaimus* and is confined to the non-muscular part of the vas deferens in *Metoncholaimus*. The paired testes are continuous with paired seminal vesicles except in *Enoplus* where the junction of posterior testis and seminal vesicle appears to have been shifted anteriad. So far as known, the spermatozoa are ameboid in the parasitic groups (Mermithoidea, Trichuroidea and Dioctophymatoidea) while in the free-living forms they are definitely flagellate as in *Trilobus*, spindle to tear drop shaped as in *Mononchus*, *Tripyla*, *Phanodermopsis*, *Enoplus* and *Actinolaimus* or rounded as in *Metoncholaimus* and *Thoracostoma*.

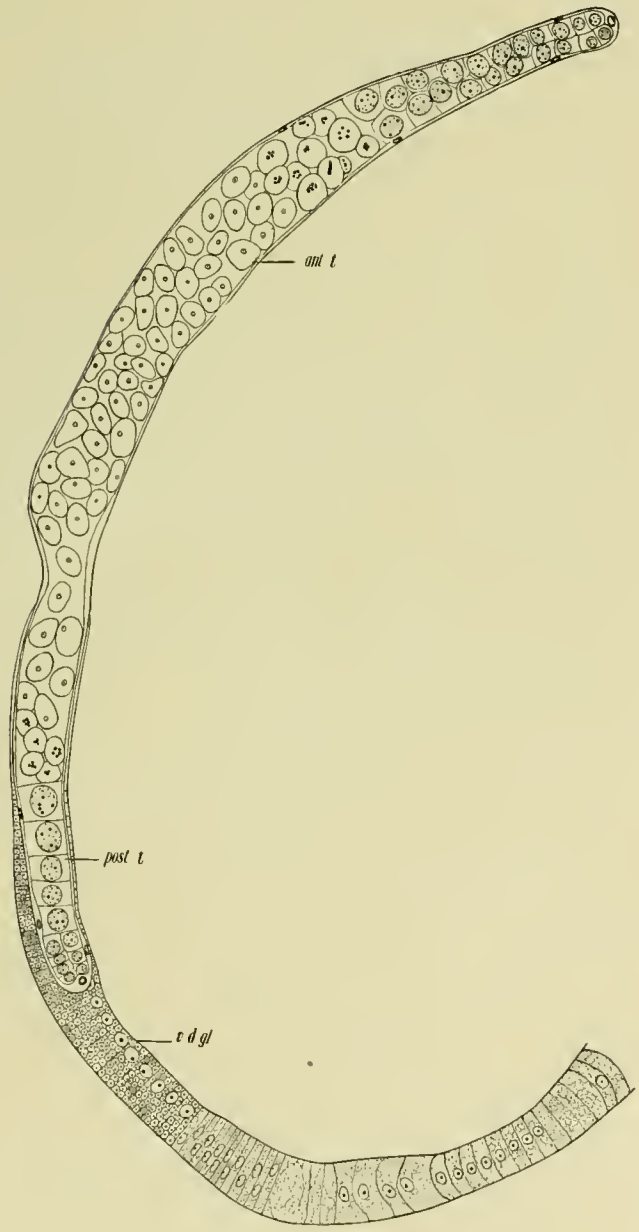

Fig. 127.

Anaplectus granulosus. Reconstruction of male reproductive system. Original.

*Cobb (1928) described the "Gametogenesis" of *Spirina parasitifera* by including in the sperm development the formation of a 128 cell "spermatophore" due to amitotic division of the spermatid. Re-examination of this species shows that what he interpreted as the spermatid is the enormous hollow spermatozoon and what he interpreted as the nuclei of the spermatophore are secretion globules in the wall of the vas deferens. The latter are arranged in transverse rows in the narrow transversely elongate epithelial cells.

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CHAPTER XI

NERVOUS SYSTEM

B. G. CHITWOOD and M. B. CHITWOOD

Historical

Otto (1816) is credited with the discovery of the chain of ganglia in the ventral chord which we have since come to recognize as the ventral nerve. This author examined the two large ascarids, *Ascaris lumbricoides* and *Parascaris equorum*. Not long thereafter Owen (1836-39) observed the ventral nerve and preanal ganglion in *Dioctophyma renale*. Siebold (1848) reexamined *D. renale* and was able to confirm the existence of a ventral nerve but he did not see the preanal ganglion; he also described fibers from the ventral nerve to the somatic musculature. At about the same time Blanchard (1847) studying various ascaridids and filarioids ascribed a nervous function to the dorsal and ventral lines (chords) and described two cell groups on each side of the esophagus; these latter have since been identified as the paired lateral and ventral cephalic ganglia.

Meissner (1853) working on *Hexamermis albicans* described the nervous system in great detail and, considering his pioneer position, in a comprehensive and creditable manner. Briefly, he characterized the nervous system of this species as follows:

There is a central nervous system consisting of a fibrous ring around the esophagus and connecting four submedian anterior ganglia, two lateral ganglia and two posterior ventral ganglia (He termed this group of structures the brain) *and three posterior ganglia at the tail. The lateral and anterior submedian ganglia supply the six anterior nerves to the six cephalic papillae* (Now recognized as the amphids and various cephalic papillary groups rather than individual papillae). *Posteriorly there are four longitudinal nerves, a dorsal, two lateroventral, and one ventral. Of these the dorsal originates directly from the fibrous ring while the other three originate as two subventral nerve trunks which unite posteriorly as the ventral nerve from which the lateroventrals branch off. Three of these longitudinal nerves are connected posteriorly with ganglia. The somatic musculature is connected with the longitudinal nerves, the nerve processes and the muscle cells merging so that one cannot say where one begins and the other ends.*

So far as this description goes it is reasonably accurate but, as we shall see later, it received a great deal of criticism.

Wedl (1855) saw the nerve ring in various parasitic nemas but mistook the sarcoplasmic part of the muscle cells for ganglion cells. Walter (1856, 1862) saw the nerve ring and associated ganglia of *Cosmocerca trispinosa;* he also saw the lateral, ventral and dorsorectal ganglia at the posterior end. But he confused the nervous system with other structures. Schneider (1860) stated that the nerve ring is the central organ and that structures described by other authors either were not present or were misidentified. Bastian (1863) described two "ganglionated chords" (now recognized as the lateral chords) as the nervous system of *Draconeulus medinensis*. Schneider (1863) redescribed the nervous system of *Parascaris equorum* as having a central organ or brain in the form of a circumesophageal commissure, the nerve ring, from which six anterior nerves extend to the cephalic sensory organs and two subventral branches to the ventral chord. Ganglion cells were seen in the six anterior nerves but it was noted that the lateral nerves were not connected with the nerve ring. (This difference is of fundamental importance and is further discussed on p. 162. He further stated that no special ventral nerve exists and criticized Meissner, Wedl, and Walter severely, stating that the transverse processes from the muscles to the median chords were muscles and that the cells seen were not nerve cells. Bastian (1866) confirmed Schneider's observations and further noted that the nerve ring usually has an inclined position with the dorsal side most anteriad. He also noted that processes from the muscle cells anterior to the nerve ring enter the nerve ring directly while those posterior to the nerve ring join the dorsal and ventral nerves. Bastian furthermore described lateral and ventral ganglia posterior to the nerve ring. Thereafter Schneider (1866) admitted the existence of median nerves.

Bütschli (1874) reinvestigated *Ascaris lumbricoides* and *Parascaris equorum* recognizing the six anterior sensory nerves with their ganglia and the lateral and ventral ganglia connected with the nerve ring. He found that some of the fibers of the lateral cephalic nerve passed the nerve ring, entered the lateral ganglia and continued through a hypodermal commissure (Cephalic lateroventral commissure I) to the nerve ring by way of the subventral nerve trunks. Bütschli also discovered first, the laterodorsal somatic nerves which originate from the dorsal part of the lateral ganglia; second, the lateroventral somatic nerves which originate from the subventral nerve trunks; and third, the ventrolateral somatic nerves which originate in the lateral ganglia and innervate the deirids or cervical papillae. In the posterior part of the body he found that the fibers from the nerve cells of the genital papillae are connected with the ventral nerve via the hypodermis. He concluded by stating that the question whether the transverse processes from the muscles to the nerves are of muscle or of nerve tissue remained unsettled but that its function seemed clear.

Rohde (1883-1885) discussed the nervous system of the tail of *Ascaris* stating that the ventral nerve bifurcates anterior to the anus at which level there is a hypodermal commissure (preanal lateroventral commissure) to the lateral ganglia (lumbar ganglia) and a pair of internal commissures passing around the rectum. Joseph (1882-1884), Rohde's former teacher, attempted to claim this as his own work but the documentary evidence is sufficient to convict him of plagiarism. He obviously knew nothing about nematodes as is evidenced by his single other paper (1879) on this matter in which he identified a worm as *Anaplectus granulosus*, giving no description but remarking on its unusual size for a free-living nema (9 to 13 mm. long). This bears on our case since he later referred to the ventral nerve as being double in the same species. For various reasons, we shall later show (p. 162) that this (double ventral nerve) must have been the primitive condition just as Meissner (1853) first indicated, but Joseph's publications should be ignored.

Hesse (1892) working on *Parascaris equorum* established the remaining general features of the nervous system topography as we know them today. To Bütschli's findings in the anterior part of the body Hesse added several more hypodermal commissures including the lateroventral commissure II. In the mid-region of the body of the female he discovered 30 dorsoventral hypodermal commissures on the right side, 12 on the left, while in the male he found 32 on the right side and 13 or 14 on the left. In the mid-region of the body of both sexes he saw a pair of dorsolateral papillae (postdeirids Fig. 128) connected with the lateral nerve and thence with the ventral nerve. In the caudal region he observed that the bifurcate ventral nerves unite with the lateral nerve by way of the preanal lateroventral commissure. The lateral caudal nerves formed by this union innervate the so called "caudal papillae" of the female (phasmids). In the male the preanal papillary nerve fibers join first the lateral nerve where a ganglion cell is located thence they return through the hypodermis to the ventral nerve by the genito-papillary commissures. All later contributions concerning the nematode nervous system are to be characterized as refinement work since no new major points in the topographic anatomy of the nervous system were added.

Topographic Anatomy

The most thoroughly studied species are, of course, *Ascaris lumbricoides* and *Parascaris equorum* due to the investigations of numerous early workers including Hesse (1892) and concluding with Goldschmidt (1908). We shall describe the anatomy as found by those workers in *Ascaris* in order to have a point of departure. The nervous system is divisible into four parts; the central, the peripheral, the recto-sympathetic and esophago-sympathetic systems. The latter has already been described (p. 95); it is connected with the central nervous systems by a pair of ventrolateral nerve fibers extending anteriad from the nerve ring.

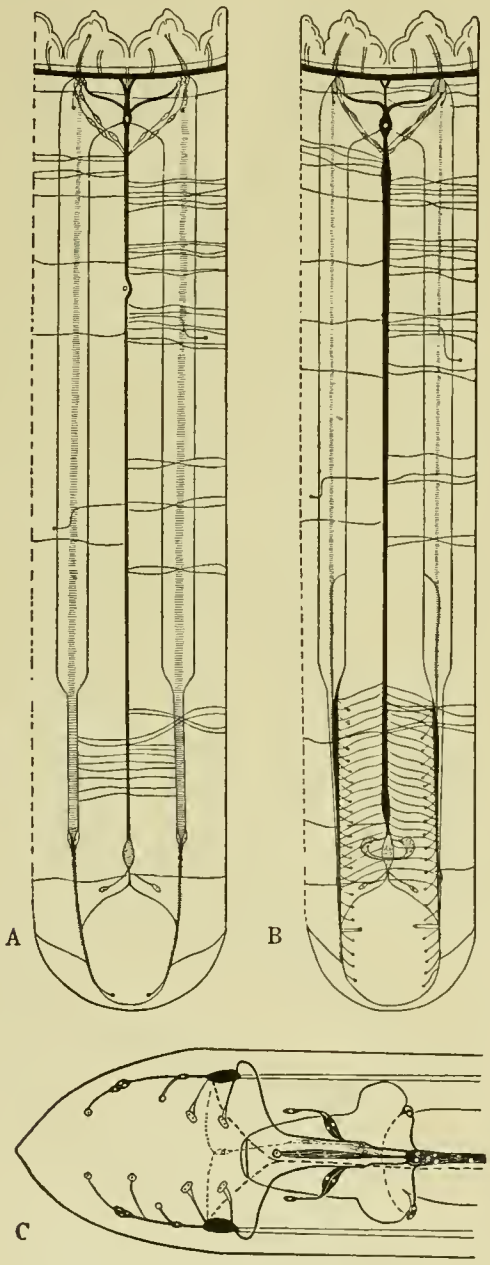

Fig. 128

Diagrams of nervous system of *Ascaris*. A—Female dissection, ventral view. B—Male dissected, ventral view. C—Male tail, reconstruction (preanal papillae omitted). A-B after Brandes 1899, Abhandl. Naturf. Gesellsch. Halle, v. 21. C—Based on Voltzenlogel, 1902, Zool. Jahrb. Abt. Anat., v. 16 (3): 481-510.

CENTRAL NERVOUS SYSTEM. We classify as central nervous system the ganglia connected with the nerve ring, the nerve ring, and the ventral ganglion chain which is termed the ventral nerve. Attached to the anterior side of the nerve ring there are six small *cephalic papillary ganglia*—two subdorsal, two lateral and two subventral (Fig. 129 D). Fibers from the posterior side of these ganglia pass directly into the nerve ring while fibers from the anterior side form the six cephalic papillary nerves. These nerves may be compared with the cranial nerves of vertebrates since their cells are situated in the chief part of the central nervous system. Anterior to the nerve ring there is also a commissure connecting the dorsal and ventral sides of the nerve ring; this asymmetric commissure consists of a nerve fiber extending anteriad from the dorsal side of the nerve ring in the dorsal chord half way to the anterior end, then turning right, through the hypodermis to the ventral chord, thence posteriad to the anterior face of the nerve ring; this is called *dorsoventral commissure* I. Attached to the posterior side of the nerve ring there is a small *dorsal ganglion* in which the *dorsal somatic nerve* originates; there are also two small *subdorsal ganglia* and two large *ventral ganglia*. In the lateral area in the region of the nerve ring there are two large masses of nerve cells which are generally referred to as the *lateral ganglia*. Their neurones are of many different types and their fibers connect with the nerve ring in various ways. Sometimes, as in *Ascaris*, the lateral ganglia may be subdivided. Goldschmidt termed the groups of lateral cells which lie directly against the nerve ring and connect with it, the *internal lateral ganglia*. There is a pair of large hypodermal commissures, the *major lateroventral commissures* connecting the major part of the lateral ganglia with the nerve ring by way of the massive paired *subventral nerve trunks*. Several subdivisions of the lateral ganglia have processes into these commissures. The largest are the *amphidial ganglia* which connect anteriad with the amphidial nerve, the others being the *posterior internolateral ganglia* and the *anterior externolateral ganglia*. The other two subdivisions of the lateral ganglia, the *median* and *posterior externolateral ganglia* are connected with the ventral nerve through a second pair of hypodermal commissures, the *minor lateroventral commissures*. One of these, the median externolateral, is also connected anteriad with the nerve ring. After giving off the major lateroventral commissures the subventral nerve trunks unite forming the ventral nerve which is in reality a chain of ganglia. The first and largest of these is called the retrovesicular ganglion; it is situated just posterior to the excretory pore at some distance posterior to the minor lateroventral commissures. Throughout the body asymmetrically placed *dorsoventral commissures* connect the dorsal and ventral nerves. A pair of symmetric dorsoventral commissures, the *anterior dorsoventral commissures*, originates from the anterior side of the nerve ring at a point posterior to where it joins with the major lateroventral commissure. There is also an asymmetric dorsoventral commissure passing by the posterior externolateral ganglion and proceeding anteriad to join the ventral nerve near the ventral ganglia; this is called the *oblique dorsoventral commissure*. Since all of these structures are rather closely associated with the nerve ring, they may be classified as central nervous system. Further groups of cells of nervous character are found throughout the length of the ventral nerve, groups being distinct in some species though not in *Ascaris*. The ventral nerve passes to the right of the excretory pore and vulva. Posteriad it gives off two internal branches, the *rectal commissures*, which extend through the body cavity and unite dorsal to the rectum; in the course of each of these commissures there is a *latero-rectal ganglion*. There is a *dorso-rectal ganglion* where the two commissures unite and from it the *median caudal nerve* extends posteriad first in the dorsal pulvillus, then in the ventral chord. Since both the commissures and ganglia are merely a branch of the ventral nerve the whole complex might be considered as a rectal sympathetic system. Posteriorly the ventral nerve ends by more or less bifid *preanal ganglia* from which the paired hypodermal *ano-lumbar commissures* extend to the lateral chords where they join the lateral nerves near the *lumbar ganglia*.

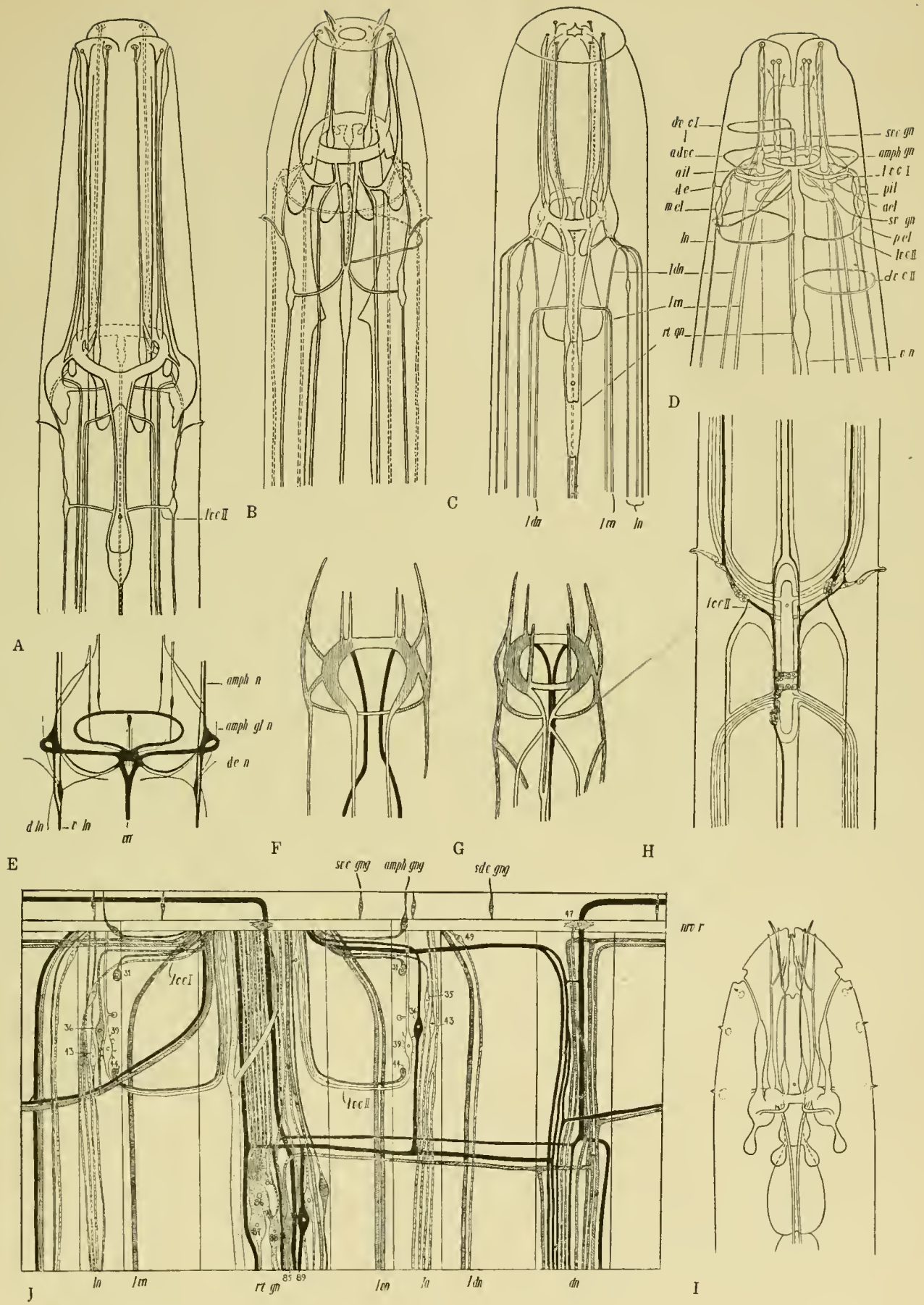

Fig. 129.

Diagrams of nervous systems. A—*Spironoura affine*. B—*Oesophagostomum dentatum*. C—*Oxyuris equi*. D—*Ascaris lumbricoides*. E—*Ancylostoma duodenale*. F—Trematoda (Central nervous system). G—Nematoda (Central nervous system). H—*Spironoura affine* (Showing postlateral ganglia and retrovesicular ganglion). I—*Siphonolaimus weismanni*. J—*Ascaris lumbricoides* (Dissection showing major nerve processes. C, based on Martini, 1916, Ztschr. Wiss. Zool., v. 116. D, after Goldschmidt, 1908, Ztschr. Wiss. Zool., v. 90. E, after Looss 1905, Rec. Egypt. Gov't. School Med., v. 3. F & G, after Martini, Deutsch. Zool. Gesellsch. a. d. 23 Jahresversamml. zu Bremen. Remainder original.

PERIPHERAL NERVOUS SYSTEM. The peripheral nervous system of nematodes consists of the *somatic nerves*, the *cephalic papillary nerves, amphidial nerves, genital papillae, cephalic papillae, amphids, deirids* and *postdeirids*.

SOMATIC NERVES. Those nerves which extend through the length of the body in the hypodermis are called somatic nerves. These include the *dorsal nerve* which originates at the posterior surface of the nerve ring with the dorsal ganglion and extends posteriad in the dorsal chord to the postanal region where it bifurcates, both branches extending through the hypodermis to the lumbar ganglia forming the *dorsolateral lumbar commissures*. Throughout its length no ganglia have been observed. It connects directly with innervation processes from the somatic muscles and is considered a motor nerve.

Laterodorsal somatic nerves originate at the dorsolateral side of the nerve ring at which point each contains one bipolar neurone. Thereafter, they extend through the hypodermis to the laterodorsal (submedian) lines where they assume a longitudinal posteriad course.

Lateroventral somatic nerves arise from the lateroventral part of the nerve ring and pass through the ventral ganglia where each has a bipolar neurone. They then leave the ventral chord with the major lateroventral commissures and reach the lateroventral (submedian) lines and extend posteriad like the laterodorsals. Neither of these paired "submedian" nerves has any ganglia in its course and like the dorsal nerve the submedians are considered motor nerves since they connect with innervation processes of the somatic musculature.

The *Ventral* nerve has already been described as part of the central nervous system and though it undoubtedly contains associational centers, it also acts as a motor nerve since it innervates the muscle cells in the subventral muscle sectors.

Dorsoventral commissures have previously been mentioned. These occur at intervals throughout the body and with one exception, the anterior dorsoventral commissures, they are unpaired and are supposed to coordinate the activity of the somatic muscles. Goldschmidt (1908) was of the opinion that the "submedian" somatic nerves were also connected with the ventral nerve by these commissures but this has not been adequately demonstrated.

Ventrolateral nerves originate from the internolateral ganglia, the anterior and the medial externolateral ganglia; the fibers from these ganglia come together posteriad and the nerves so formed extend posteriorly at the side of the excretory canal. Further ganglia have not been observed in their course until they reach the posterior extremity. In the anal region of the female each ventrolateral nerve contains a group of nerve cells called the lumbar ganglion. At approximately the same level the ano-lumbar commissure connects it with the ventral nerve. Paired lateral nerves which continue posteriad from these ganglia are called the *lateral caudal nerves*. They innervate the phasmids in the female. In the male the ventrolateral nerve (also called the *bursal nerve*) innervates the genital papillae and paired *genito-papillary commissures* connect it with the ventral nerve. Postanal genital papillae are innervated by processes from the enlarged lumbar ganglion and branches of the lateral caudal nerves. The lateroventral somatic nerve is thus seen to be at least partly a sensory nerve.

Dorsolateral nerves have been described by Hesse (1892), Brandes (1899) and Voltzenlogel (1902). Goldschmidt (1908) apparently overlooked them; they might correspond to the short processes extending posteriad from the anterior externolateral ganglia. They unite posteriad with the ventrolateral nerve in the anal region.

Cephalic papillary nerves and papillae. There are six anterior papillary nerves arising from the anterior surface of the nerve ring and extending to the anterior extremity; unlike the somatic nerves, the papillary nerves go through the body cavity, being applied closely to the external surface of the esophagus. Each of these nerves contains a ganglion (cephalic papillary) of bipolar nerve cells at the anterior surface of the nerve ring. The sensory endings of the nerves include the cephalic papillae. Each subdorsal and subventral cephalic papillary nerve terminates anteriad in a large pair of partially fused papillae (dorsodorsal and laterodorsal or ventroventral and lateroventral) of the external circle, and a small rudimentary papilla (internodorsal or internoventral) of the internal circle. The lateral papillary nerves each terminate in one large papilla of the external circle (ventrolateral) and a rudimentary papilla of the internal circle (internolateral).

Amphidial nerves and amphids. Like the cephalic papillary nerves, the amphidial nerves each innervate a cephalic sensory organ but unlike the papillary nerves their connection with the nerve ring is indirect. The nerve cells are situated in the amphidial ganglia which lie posterior to the nerve ring, and their axones pass into the major lateroventral commissures to the ventral nerve trunks before reaching the nerve ring. Anteriorly each amphidial nerve enters an *amphidial gland* and its processes break up in an elongate sac, *amphidial pouch;* the sensory elements which represent the specialized ends of individual neurones are called terminals and the group of elements is called a *sensilla*. From the pouch, anteriad, there is a short *amphidial duct* which opens to the outside at the *amphidial pore*.

Deirids. These are paired papillae in the cervical region commonly called *cervical papillae*. Each is innervated by a branch of the nerve trunk which connects the medial externolateral ganglia with the nerve ring; the sensory cell of each deirid lies in that ganglion.

Postdeirids. These are paired and asymmetrically placed papillae first seen by Hesse (1892), in the mid-region of the body. Each is innervated by a single nerve fiber connected with a sensory neurone in the lateral chord. The axone passes through the hypodermis to the ventral nerve.

Genital papillae and Connections. Each preanal genital papilla sends a nerve fiber through the hypodermis to the lateral chord where it enlarges to form a bipolar neurone the axone of which joins the ventrolateral somatic nerve and reaches the ventral nerve by way of a genito-papillary commissure. In addition there is a medioventral preanal papilla which, according to Voltzenlogel (1902) is innervated by four bipolar neurones connected directly with the posterior end of the ventral nerve. (Fig. 128 C). Posterior to the anus the genital papillae are innervated by processes of the lumbar ganglia. Of these, the first pair is double and has two nerve fibers.

Phasmids are known to occur in both sexes of *Ascaris* and to be innervated by processes of the lateral caudal nerves but no further details have been obtained.

Topographic Anatomy of the Nervous System of Species Other Than Ascaris

The nervous systems of only a few other nematodes have been studied, namely: *Siphonolaimus weismanni* by zur Strassen (1904), *Ancylostoma duodenale* by Looss (1905), *Hexamermis albicans* (syn. *Mermis albicans*) by Rauther (1906), *Oxyuris equi* by Martini (1916), *Rhabditis strongyloides* by Chitwood (1930), *Camallanus* spp. and *Cucullanus heterochrous* by Törnquist (1931), *Cephalobellus papilliger* by Chitwood and Chitwood (1933) and *Rhabditis terricola* by Chitwood and Wehr (1934). In preparing this volume we have made a point of studying two additional species, *Spironoura affine* and *Oesophagostomum dentatum*. Restudy of *Rhabditis strongyloides* has shown that trust was misplaced in the use of methylene blue as an intravitam stain and the publication in which it was described (Chitwood, 1930) contains so many gross errors that it should be ignored. The correct form of the nervous system of *Rhabditis* is shown in Fig. 8. The general features of the nervous system in all the forms studied is very similar even though they represent considerably diverse groups.

Central nervous system. Differences in the central nervous system lie chiefly in the degree of subdivision of the lateral ganglia, the form of the ventral ganglia and degree of fusion of the ventral nerves.

In *Siphonolaimus weismanni* (Fig. 129 I) the ventral nerves are paired as far as they have been traced but this tracing did not extend so far as the retrovesicular ganglion. In *Ancylostoma duodenale, Oesophagostomum dentatum, Spironoura affine, Cephalobellus papilliger,* and *Rhabditis terricola* they are fused in the retrovesicular ganglion and thereafter are apparently single but, considering the minuteness of the left fiber group, doubleness of the ventral nerve might be overlooked. In *Oxyuris equi* (Fig. 129 C) Martini found the ventral nerves paired to the posterior side of the vulva which happens to be situated distinctly pre-equatorial in this species. In the other species the ventral nerve passes to the right side of the vulva. Both Martini (1916) and Chitwood and

Chitwood (1933) have enumerated the cells found in the ventral nerve between the retrovesicular ganglion and the posterior *preanal ganglion* but neither found sufficiently clear grouping of the cells to warrant establishment of a series of named ganglia; comparing their work with the situation in *Spironoura* (Fig. 132 D) we find that there are 25-30 neurones of which a group of 6-7 form a postvulvar ganglion, that sometimes there is a more or less distinct prevulvar ganglion and that other neurones may or may not be grouped. Looss found a vaginal nerve, originating from the prevulvar ganglion, which forms a commissure around the vagina at its juncture with the uteri. The same author also described paired *anal nerves* originating in the paired preanal ganglia and extending posteriad to the anterior lip of the anus (Fig. 130 AA). At the preanal ganglion the ventral nerve is double in *Ancylostoma duodenale, Oxyuris equi* and *Rhabditis terricola*. The apparent doubleness in both anterior and posterior ends of the ventral nerve caused Meissner and many later authors to conclude that the entire ventral nerve was at one time double. Arguments against this view have been based on the fact that in most nemas studied the ventral nerve goes to the right of the vulva instead of dividing to go around it. *Oxyuris equi* is a conspicuous exception in this latter respect but here it might be argued that the vulva is shifted anteriad. As Looss pointed out, the asymmetric vulvar by-pass is to be expected in developmental anatomy since the ventral nerve is already in position when the vulva is formed. The writers subscribe to the primitive double ventral nerve hypothesis.

The ventral ganglia are each transversely lobed in *Siphonolaimus, Hexamermis*, and *Rhabditis* the smaller lobes being called the postventral ganglia, the term ventral ganglia being reserved for the anterior lobes. In other nemas studied, the ventral ganglia are not subdivided.

The lateral ganglia are more or less lobed in all nemas, but in none thus far studied are they subdivided into as many parts as in *Ascaris*. As a general rule there is a lobe forming the *dorsolateral ganglion* connected with the nerve ring near the origin of the laterodorsal and dorsolateral somatic nerves. The term *lateral ganglion* is reserved for the major part of the lateral ganglion while a posterior lobe, the postlateral ganglion is some distance from the major ganglion group; it connects anteriorly and posteriorly with the ventrolateral somatic nerve and ventrally with the minor lateroventral commissure.

Somatic Nerves. The dorsal somatic nerve and ventrolateral somatic nerves in the genera studied are similar to those of *Ascaris* with the exceptions that in *Camallanus* and *Cucullanus* Törnquist identified several nerve cells in the course of the dorsal nerve and in those forms without deirids (*Oxyuris, Hexamermis, Cephalobellus* and *Siphonolaimus*) the ventrolateral nerve has no branch to the surface. A dorsolateral nerve has been seen only in *Ancylostoma* and *Oxyuris* and submedian somatic nerves in *Cephalobellus, Spironoura, Rhabditis, Hexamermis* and *Oesophagostomum*. Numerous dorsoventral commissures, such as Hesse describes in *Ascaris* have not been seen in any of the other forms studied. The two anterior lateroventral commissures, the rectal and anal commissures are the only ones known to be generally existent.

Cephalic papillary nerves and *papillae*. There are always six cephalic nerves connected posteriad with six papillary ganglia and anteriad with six groups of papillae. Törnquist (1931) observed these nerves and ganglia but was unable to find the lateral cephalic papillary group and confused the fibers and ganglia with the amphidial nerve and lateral ganglia respectively. The papillae have been previously described (pp. 55-64) in these and other forms so that there is no need of repeating the discussion here. We need only call to the readers' attention that there are primarily three papillae in each submedian group and two in each lateral group. Among parasitic phasmidians there is a general tendency for the internal circle of papillae to become reduced or rudimentary. There is also a tendency toward reduction of the external circle either through reduction of the externomedial papillae or through the joining of the lateromedial papillae. The ventrolateral papillae may or may not become reduced or rudimentary coincident with reduction of the mediomedials.

Amphidial nerves and amphids are fundamentally like those of *Ascaris* in all forms.

Enumerative and Minute Anatomy

CEPHALIC PAPILLARY GANGLIA, NERVES, PAPILLAE AND ASSOCIATED CELLS. Goldschmidt (1903) worked out the cephalic papillary nervous system of *Ascaris* along with the non-nervous cells of the anterior end. We have already discussed many of the non-nervous cells (p. 37) but because of their rather intimate association with the papillary nerves some repetition will be necessary.

Arcade Cells. These are apparently hypodermal cells of the stomatal and labial regions. Nine such cells have been found in *Ascaris* (Goldschmidt, 1903, and Hoeppli, 1925), *Oxyuris* (Martini, 1916), *Strongylus* (Imminck, 1924), *Cephalobellus* (Chitwood & Chitwood, 1933), and *Rhabditis, Spironoura* and *Oesophagostomum* (this publication). They are not connected in any way with the nervous system but must be distinguished from it. In all except *Strongylus, Oesophagostomum* and *Spironoura* they take the form of elongate, posteriorly directed cells united anteriad in a transverse plate opposite the base of the labial region. Their cell bodies are closely applied to the esophageal surface, distributed as follows: one dorsal, four dorsolateral, two ventrolateral and two ventral (Fig. 46 A-B). In *Strongylus* (Fig. 46 E) they are distributed in the same pattern but are confined to the stomatal region and take the form of three protoplasmic bands. In *Oesophagostomum* they are situated in the body cavity but at the level of its nucleus each cell has a process inserting it into the hypodermis next to the chord with which it is associated. There are two subdorsal arcade cells beside the dorsal chord, one dorsolateral on the left side and two on the right side next to the lateral chord, one on each side ventrolateral next to the lateral chords and two subventral on the right side of the ventral chord. In *Spironoura* the arrangement is more nearly typical but instead of there being four dorsolateral and two ventrolateral there are two dorsolateral and four ventrolateral.

Non-specific Connective tissue. There may be several types of connective tissue cells not associated with the nervous system but situated in the body cavity around the esophagus. In *Ascaris* Goldschmidt listed three fibril cells opposite the three esophageal radii and two "Füllzellen" (left dorsolateral and subventral) and in *Oxyuris* Martini listed three "Bindegewebe" cells, one dorsal and two ventrolateral, in addition to those already mentioned. In *Oesophagostomum* the three fibril cells have been observed but other cells could not be identified.

Submedian Papillary Ganglia, Nerves and *Papillae*. In *Ascaris* Goldschmidt (1903, 1908) found each of these ganglia to be composed of seven bipolar sensory neurones (Cells 50-56 times 2, subventral, and cells 57-63 times 2 subdorsal, Fig. 130 G). Posteriad a process from each cell enters the nerve ring while anteriad they come together forming the submedian papillary nerves. In addition to the nerve processes a glia process enters the corresponding nerve from each of the four giant glia cells situated on the anterior surface of the nerve ring (Fig. 130 C).

Anteriorly the processes of four of the neurones stop in the postlabial region while the other three innervate papillae. The fiber innervating each lateromedian papilla (laterodorsal or lateroventral) anteriad becomes ensheathed by the glia process from the corresponding *glia cell* on the nerve ring and this is in turn partially surrounded by an *escort cell*, the two together forming the papillary mass. At its termination the cuticle has a very deep invagination from which a fine sensory hair projects; the hair is continuous with the dendritic process of the nerve (Fig. 130 L). The medio-medial papillae are each formed by a glia and escort cell; in this case the nucleus of the glia cell (Fig. 130 P) is some distance anterior to the nerve ring. The sensory terminus differs from that of the lateromedial papilla in that it ends under the surface in a sensory plate or receptaculum (Fig. 130 L). A clavate cell accompanies each of the submedian papillary nerves but is not associated with either of the processes to the external circle of papillae; it may, perhaps, act as an escort cell of the fiber to the internomedial papilla. This papilla is greatly reduced in *Ascaris*; Hoeppli (1925) described a special glia cell for this structure. The clavate cell acts as its escort cell.

In *Oxyuris*, Martini (1916) found three neurones (Cells 50-52 times 2 in Fig. 131 B) in each subdorsal papillary


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AA
BB
dch
lch
tch
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ac
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pl u
m lu
mt lu
pb
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Fig. 130.

ganglion and two glia cells (Cells 53 times 2 and ct. 7-8 in Fig. 131 B) disposed in the same manner as the glia cells of *Ascaris*. The cell whose fiber enters the nerve ring between the other two (Cells 52) becomes surrounded anteriorly by the clavate cell and then terminates as an internomedial papilla; no glia cell is associated with it. The cell whose fiber enters the nerve ring most laterally (Cell 50) retains this position throughout its course, becoming associated first with the glia cell (Cell 53), then the escort cell (Hügelzelle), all three together then forming the large laterodorsal papilla. The cell whose fiber enters the nerve ring most dorsally is probably supplied by glia tissue from the cell on the nerve ring (Ct. 7-8) for no other glia or escort cells are associated with it. It terminates under the cuticle as the rudimentary dorsodorsal papilla. The subventral papillary ganglia are similar to the subdorsal except that there are two cells connected with the ventroventral rudimentary papillae; one of these might be a glia cell.

In *Spironoura* we have found five bipolar neurones in each of the subdorsal and subventral papillary ganglia. With these, three glia and four escort cells are associated. In addition a submedian glia cell at the surface of the nerve ring also has a process into each nerve. Three of the neurones with corresponding glia and escort cells form the three well developed papillae in which each of these nerves terminate. The ultimate destination of the two other neurones and the extra glia and escort cells is unknown. In addition to the neurones just described each subventral nerve receives processes from two bipolar neurones in the region of the lateral papillary ganglia (Fig. 131 J); presumably they innervate the esophago-sympathetic system.

In *Oesophagostomum* each subdorsal papillary ganglion contains only four bipolar neurones while the subventral contain five. (Fig. 132 A). As in *Spinonoura* seven cells in addition to the anterior glia cell of the nerve ring are associated with each papillary nerve, three glia cells and four escort cells. Anteriorly each nerve terminates in a reduced papilla of the internal circle and a conoid (double) papilla of the external circle (Fig. 129 B).

Lateral papillary ganglia. In *Ascaris*, Goldschmidt (1903, 1908) found four bipolar neurones (Fig. 130 D Cells 64-67), one glia cell, one escort cell and one clavate cell. Two of these neurones (Cells 66-67) innervate the ventrolateral papilla but only one is surrounded by the glia and escort cells. The most ventral cell (66) is the one surrounded by glia and forms the bulk of the sense organ; it ends in a plate or receptaculum (Fig. 130 K) like those of the medial papillae. The other fiber (67) ends under the cuticle without any special sensory terminus and must, therefore, be considered rudimentary. The most anterior cell (64) becomes associated with the clavate cell and presumably innervates the greatly reduced internolateral papilla.

In *Oxyuris*, Martini (1916) recorded four bipolar neurones (Fig. 131 D) connected with the nerve ring, in each of the lateral papillary ganglia (Cells 11, 14, 18 and 19); with these cells two glia cells (12 and 17) and one clavate cell are associated. The most ventral of these (19) is probably supported by the corresponding glia cell (17); it terminates anteriorly under the cuticle as the rudimentary ventrolateral papilla. The most dorsal (11) is associated with the glia cell (12) and the clavate cell and terminates anteriad as the greatly reduced internolateral papilla.

In *Spironoura* there are likewise four bipolar neurones (Fig. 131 K) in the lateral papillary nerve but in addition two glia and three escort cells were observed. The most dorsal neurone innervates the internolateral papilla and is associated with the most anterior glia and escort cells while the most ventral neurone innervates the well developed ventrolateral papilla and is associated with the other glia cell and at least one of the escort cells. The lateral papillary ganglia of *Oesophagostomum* contain only three bipolar neurones which become associated with two glia and no escort cells. The nerve innervates the greatly reduced internolateral and rudimentary ventrolateral papillae.

It seems obvious from the comparative anatomy that escort cells (including clavate cells) are definitely correlated with papilla formation. In *Ascaris* and *Oxyuris* the number of such cells associated with each nerve is the same as the number of papillae reaching the body surface, for the lateral nerve two in *Ascaris* and one in *Oxyuris* and for the submedian nerves three in *Ascaris* and two in *Oxyuris*. In *Oesophagostomum* there are none laterally and no distinct papillae. However the submedian nerves of both *Spironoura* and *Oesophagostomum* have four escort cells, though there are but three papillae in *Spironoura* and one very large papilla in *Oesophagostomum*. We have previously seen (p. 56) that the large conoid papillae of *Oesophagostomum* are double; in addition we have found a small internomedial papilla. This would leave one escort cell unaccounted for in both *Spironoura* and *Oesophagostomum*. The reason for variability in number of glia cells is not apparent, neither is the variation in the number of neurones. Three neurones are required for papillary innervation and these are always present, even in the lateral nerve. If we may judge by Goldschmidt's work on the ventrolateral papilla (Fig. 130 K) we cannot help but conclude that a dorsolateral papilla (homologous to the lateromedial papillae) was present in ancestral forms. The additional cell in the subventral ganglia of *Oesophagostomum* probably connects with the esophago-sympathetic system; the cells which have this function in the other genera studied have been omitted from the descriptions. The neurones not connected with papillae in *Ascaris* and *Spironoura* must end in the lip tissues.

NERVE RING. The nerve ring is an associational structure where processes from the many ganglia of the central nervous system come into direct relationships with one another. Goldschmidt believed its primary function was to correlate motor impulses entering the various motor nerves but he did not preclude the association of sensory impulses.

In *Ascaris* there are eight cells which must be classified as cells of the nerve ring. Four of these are the anterior glia cells which send processes into the submedian papillary nerves. The other four cells, numbered 46 (paired lateral), 47 (unpaired dorsal) and 48 (unpaired ventral) are associational neurones (Fig. 130 I). These four cells have direct continuity with each other and with various motor neurones, with motor nerves and with commissural cells of the lateral ganglia. Several of the unipolar central cells (21, 27, 29) were found to divide after entering the nerve ring, having one process dorsad, the other ventrad (Fig. 134). Goldschmidt reconstructed portions of the dorsal, ventral, and lateral areas of the nerve ring (Fig. 133, 134) showing the direct anastomoses of many of the fibers. However, he was able to identify particular fibers with cells only in some instances (those labelled Z 21 etc.) in which the number corresponds to the cell number given in other illustrations. In other instances he merely numbered the indi-

Fig. 130.

Details of nervous system. A-Z—*Ascaris lumbricoides* (except K-Q, *Porascaris equorum*). (A—Ventral ganglion; B—Dorsal ganglion; C—Subventral cephalic papillary ganglion; D—Amphidial and internal lobes of lateral ganglion; E—Diagrammatic representation of the tripolar neurones from which fibers of the laterodorsal (49) and the lateroventral somatic nerves originate; F—External lobe of lateral ganglion; G—General dissection of central nervous system as seen from inside, ventral chord median; H—Subdorsal ganglion (Glia cells white); I—Diagram of commissural connections of nerve ring (47 dorsal), lines posterior connect with innervation processes and somatic nerves; J—Cells 80, 86, 87 and 88 of the retrovesicular ganglion showing cells in direct continuity; K—Ventrolateral papilla showing two nerve endings, upper one forming standard papilla, lower one rudimentary; actually the lower is supposed to represent the rudimentary dorsolateral, the upper the well developed ventrolateral; L—Submedian double papilla, laterodorsal to readers' right, dorsodorsal to readers' left (with receptaculum in white); M—Laterodorsal papillae showing sensory plate, only plate and terminus seen in L; N—Plate of laterodorsal papilla; O—Amphidial pouch and sensilla; P—Dorsodorsal papilla and associated cells; Q—Laterodorsal papilla and associated cells; R—Cell 46, showing glia capsule; S—Cell 51, showing neurofibril; T—Cell 25, showing radial network and neurofibrillar basket; U—Cell 67, showing neurofibrillar network; V—Cell 23, showing glia fibrils entering protoplasm; W—Cell 24, glia cell of nerve ring; X—Ventral nerve with innervation processes, methylene blue; Y—Ventral nerve with insertion of neurofibrils from innervation process; Z—Diagrammatic dissection of nervous system from which parts of nerve ring were reconstructed (Figs. 133 & 134); AA-BB—*Ancylostoma duodenale* (Diagrams of caudal part of nervous system, AA—Female, BB—Male).

Figs. A-J, After Goldschmidt 1908. Ztschr. Wiss. Zool., v. 90. K, After Goldschmidt 1903, Zool. Jahrb. Abt. Anat., v. 18 (1). R-Y, After Goldschmidt, 1910, Festschr. Hertwig, v. 2., (X, From Delneka). Z, After Goldschmidt, 1909, Ztschr. Wiss. Zool., v. 92 (2). AA-BB, After Looss 1905, Rec. Egypt. Govt. School Med., v. 3.

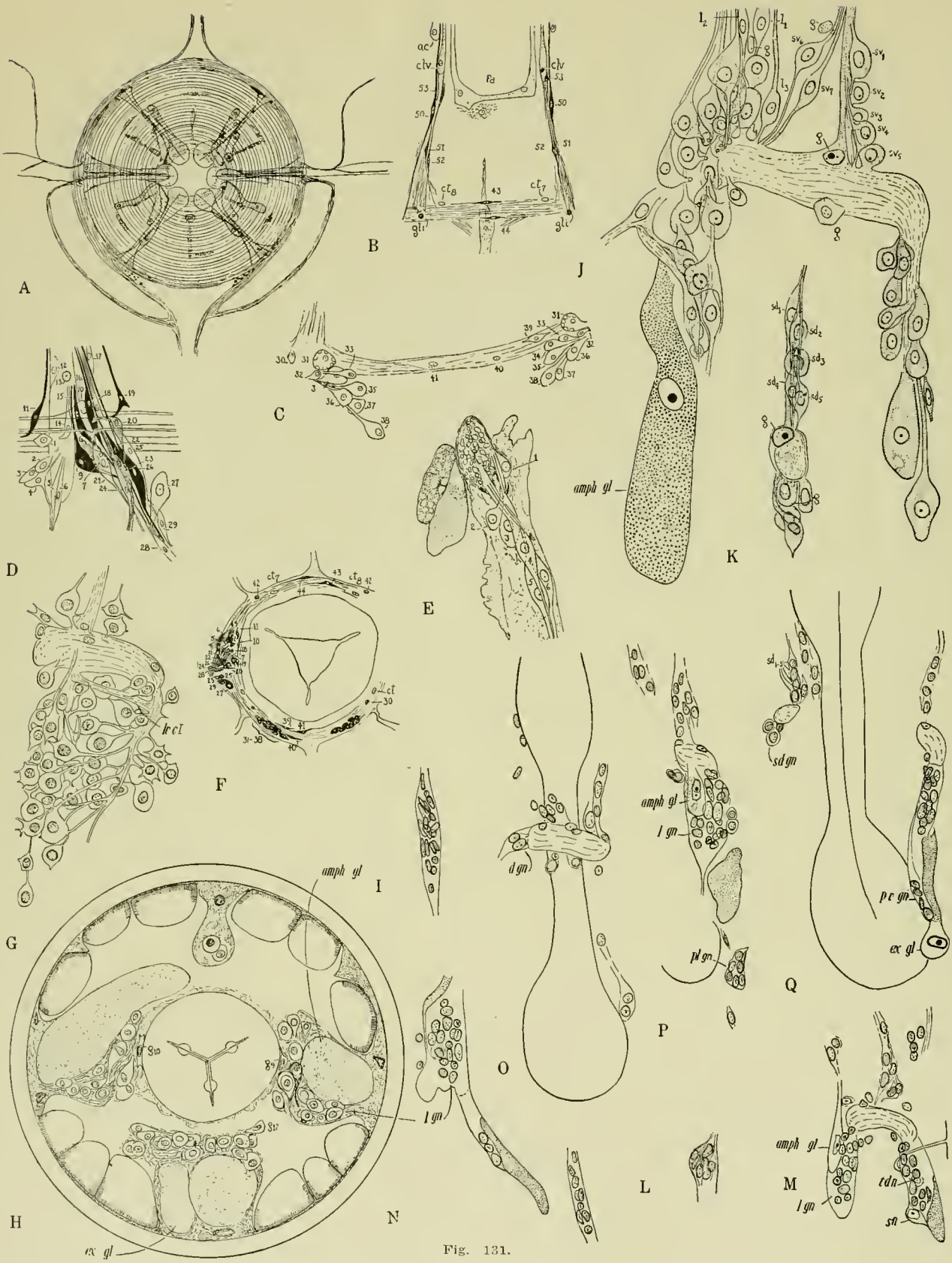

Fig. 131.

Details of nervous system. A-F—*Oxyuris equi* (A—Diagram showing cephalic part of nervous system as seen *en face;* B—Dorsal part of nerve ring and subdorsal cephalic papillary ganglia; C—Ventral part of nerve ring and ventral ganglion; D—Lateral ganglion; E—Dorsolateral lobe of lateral ganglion; F—Diagrammatic reconstruction of ganglia on level of nerve ring). G—*Metoncholaimus pristiurus* (Longitudinal section showing nerve ring and parts of lateral and ventral ganglia). H—*Oesophagostomum dentatum* (Cross section just posterior to nerve ring). I—*Rhabditis lambdiensis,* retrovesicular ganglion. J—*Spironoura affine* (Longitudinal section showing parts of lateral and ventral ganglia. Tbe lateral cells (on readers' left) which terminate as circles at level of nerve ring are amphidial neurones, the circles representing cut ends of fibers to lateroventral commissure I.). K—*Spironoura affine* (Subdorsal cephalic papillary ganglion and subdorsal ganglion). L-Q—*Rhabditis terricola* (L—Postlateral ganglion; M—Longitudinal section showing parts of lateral ventral and subventral papillary ganglia; N—Section adjoining M, shaded area to right is excretory tissue, neurones next to it are postventral ganglion cells; to right are retrovesicular ganglion cells). Q, O & P follow in series.

A-F, After Martini 1916, Ztschr. Wiss. Zool., v. 116. Remainder original.

vidual fibers for descriptive purposes (small numbers opposite fibers). The fibers of the major lateroventral commissure are labelled L 1-12, those of the ventral nerve B 1-31, those of the submedian somatic nerves Subl I-IV, 1-4, and a-d. The ordinates and coordinates are also numbered but this is merely for purposes of location. Further discussion seems unnecessary since those interested in the detail may obtain it from the illustrations.

In *Oxyuris equi* Martini (1916) found eight glia cells (ct. in Fig. 130 F) and seven commissural cells corresponding to the four described by Goldschmidt for *Ascaris*. The commissural cells are located: two lateral (cell 10 r. l.), two dorsal (43, 44) and three ventral (39, 40, 41).

In *Spironoura affine* (Fig. 131 J-K) and *Oesophagostomum dentatum* (Fig. 132 A-B) we find the same arrangement as in *Ascaris* except that in both forms there is a pair of subventral glia cells on the posterior surface of the nerve ring and in *O. dentatum* there is also a dorsal posterior and a ventral anterior glia cell.

Dorsal and subdorsal ganglia. In *Ascaris* the dorsal ganglion consists of two central cells (Fig. 130 C) each with two processes to the nerve ring while in *Parascaris equorum* one of these cells has a single process. In the latter species Goldschmidt also saw the posterior dorsal glia cell which we have mentioned on the nerve ring of *Oesophagostomum*. The dorsal ganglion of other species also contains two nerve cells which may have a very long central cylinder as in *Spironoura*; in this case they appear to be located in the dorsal nerve. Possibly this is the reason for our having found only one such ganglion cell in *Cephalobellus* and for Martini's not finding a dorsal ganglion in *Oxyuris* (an extra dorsal commissural cell probably corresponds to one of the dorsal ganglion cells of *Ascaris*).

The subdorsal ganglia each consist of two central cells in *Ascaris, Spironoura, Rhabditis* and *Oesophagostomum* and with it two glia cells are associated in the first two genera but only one in the two last named. Paired posterior subdorsal glia cells in *Oxyuris* and *Cephalobellus* were attributed to the nerve ring, but they are undoubtedly homologous to those associated with the subdorsal ganglia where such ganglia are present. Casual observation indicates that absence of subdorsal ganglia may be characteristic of the Thelastomatidae and Oxyuridae.

Lateral ganglia, Amphids and Associated Structures. In all nemas the lateral ganglia contain the largest number of cells and are so intimately associated with the amphids and deirids that it is easiest to consider them at once. In *Ascaris*, Goldschmidt found a total of 35 nerve cells while in *Oxyuris*, Martini found 21, in *Cephalobellus*, the writers found 26 cells, in *Spironoura* 42, in *Oesophagostomum* 41 and in *Rhabditis* 42.

Postlateral ganglia are absent in *Oxyuris* and *Cephalobellus* while in *Spironoura, Rhabditis* and *Oesophagostomum* they are the most clearly set apart. In *Spironoura* and *Oesophagostomum* each of these ganglia is composed of two groups of cells. The anterior group consists of two cells, one a sensory cell connected with the deirid, the other a glia cell. The second group consists of five cells all of which have processes into the minor lateroventral commissure. In *Rhabditis* all seven cells are in one group (Fig. 131 P).

The postlateral and mediolateral ganglia of *Ascaris* contain cells corresponding to those found in the postlateral and mediolateral ganglia of other genera studied but the grouping differs. Since Goldschmidt's grouping in the case of *Ascaris* is rather artificial, there being no distinct lobes in that species, we shall regroup the cells he described. The internolateral ganglia are in close association with the amphidial ganglia and cannot be grossly distinguished from them. Goldschmidt subdivided the internolaterals into anterior and posterior lobes, but this division is not practical. Each whole internolateral ganglion contains eleven cells, seven being unipolar with a process to the nerve ring (23-29), three unipolar with a process to the major lateroventral commissure (30-32) and one (49) tripolar with one process to the nerve ring, one to the ventrolateral nerve and one to the dorsosubmedial nerve.

In *Ascaris* the amphidial ganglia (Fig. 130 D) each contain 11 sensory neurones (68-78) connected anteriorly with the amphidial nerve and posteriorly with the major lateroventral commissure. The amphidial gland lies dorsal to the amphidial ganglion and extends anteriad eventually surrounding the amphidial nerve. At this level (slightly posterior to its terminus) the amphidial gland duct attains a cuticular lining and is slightly dilated forming the *amphidial pouch*. Within this structure there is a *sensilla* consisting in *Ascaris* of 11 rod-like sensory *terminals* (Fig. 130 O). The lumen of the pouch is in direct continuity with a short tube leading to the amphidial pore.

The externolateral lobes of the lateral ganglia were subdivided by Goldschmidt into three parts, the anterior, medial and posterior parts but since there is no real subdivision (Fig. 130 F) we will describe these structures as a single unit. Each whole ganglion contains 13 cells of which eight are unipolar, four have a process to the nerve ring (37, 40, 41, 42), two have a process to the major lateroventral commissure (33, 34) and two have a process to the minor lateroventral commissure (44, 45). The five bipolar neurones have processes as follows: two (38, 43) have processes to the nerve ring and ventrolateral nerve; one (35) has a process to the major lateroventral commissure and another to the lateral nerve; one (39) has a process to the nerve ring (Fig. 130 E) and another to the minor lateroventral commissure (a side branch of this process innervates the deirid); and one (36) has its anterior process to the nerve ring, its posterior process entering the oblique ventrodorsal commissure (right side) or the ventrodorsal commissure II (left side).

Martini (1916) found only two subdivisions of the lateral ganglia in *Oxyuris*, these being the dorsal and ventral lobes (Fig. 131 D). The dorsal lobe contains six neurones, three unipolar to the nerve ring (1-3) and three bipolar with one process to the nerve ring and the other to the common root of the laterodorsal, dorso- and mediolateral somatic nerves. The ventral lobe consists of 15 cells, five of which are bipolar, innervating the amphids and passing through the latero-ventral commissure; the latter (9, 15, 16, 22, 26) undoubtedly correspond to Goldschmidt's amphidial ganglion (11 cells in *Ascaris*). Of the remaining 10 neurones, two are unipolar to the nerve ring (7-8), one is unipolar to the lateroventral commissure (27), three are bipolar with processes to the ventrolateral somatic nerve and the nerve ring (20, 23, 24) and four are bipolar with processes to the lateroventral commissure and the nerve ring. The mediolateral nerve has three neurones in its course, two far back in the body region and one not far distant from the lateral ganglia. The latter might be considered part of the lateral ganglion, possibly representing a rudimentary postlateral lobe.

The writers (1933) found no marked subdivision but a distinct tendency toward separation of an amphidial and a dorsal lobe as well as a rudimentary postlateral lobe of the lateral ganglion in *Cephalobellus*. The chief lobe contained three unipolar cells to the nerve ring (4, 12, 17), two unipolar cells to the lateroventral commissure (20, 23), six cells of undetermined character (14, 16, 18, 21, 22), and a glia cell (8). The dorsal lobe contained two unipolar cells to the nerve ring (6, 7) and three bipolar cells to the nerve ring and dorsosubmedian lateral nerve trunk. The amphidial lobe contained eight bipolar cells to the lateroventral commissure and amphid (13, 19, 24-28, N). The postlateral lobe contained two neurones (29, 30) attached to the lateral nerve.

In *Spironoura* there is a very distinct division of the lateral ganglia into anterior and posterior lobes, the anterior lobe containing 35, the posterior lobe seven cells. In the anterior lobe subdivision is indistinct. The courses of only part of the cells have been traced; of these six are unipolar direct central cells, seven are unipolar cells entering the major lateroventral commissure, eight dorsolateral cells are connected with the dorsosubmedian and lateral nerve trunk and eight are connected with the amphidial nerve and lateroventral commissure. The amphidial glands (Fig. 131 J) are particularly massive in this form. In the postlateral ganglion only six of the cells are neurones, the seventh being the glia cell of the deirid. At least three, possibly four neurones are bipolar with anterior processes in the lateral nerve and posterior processes through the minor lateroventral commissure (one of these has a branch to the deirid); another of the cells is bipolar with one process anterior and another posteriad entering the lateral nerve, while the sixth appears to be tripolar, with two processes entering the lateral nerve and a third the dorsolateral commissure.

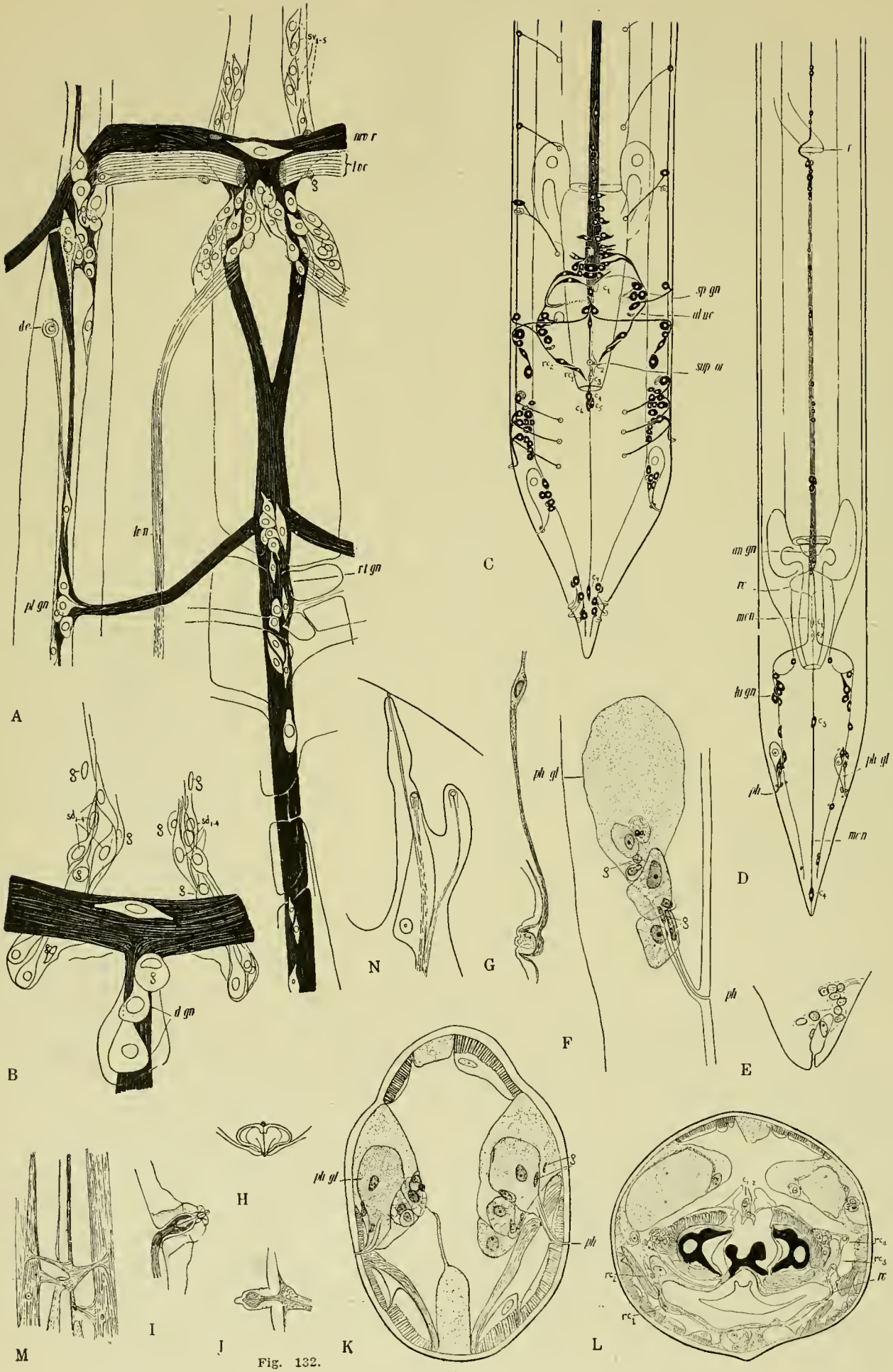
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Fig. 132.

In *Ocsophagostomum* and *Rhabditis* practically the same subdivision of the lateral ganglia (seven cells in postlaterals) has been observed except that in *Ocsophagostomum* the dorsoventral commissure originates with the dorsosubmedian nerve.

Metoncholaimus pristiurus (Fig. 131 D) is the only aphasmidian that we have casually studied and no exact information is available. However, considering Filipjev's (1912, 1934) indication that the nervous system is basically different in aphasmidians it is interesting to note the same general arrangement in the lateral ganglion with many cells entering the lateroventral commissure. The cells are not so closely packed but there is no other obvious difference.

Ventral Ganglion. In *Ascaris* the ventral ganglion (Fig. 130 A) is bilobed and contains 33 cells of which 15 are paired and three unpaired, cell 16 being medial (on right side in figure) and cells 17 and 18 on the right side. All except two cells are unipolar and the bipolar exceptions innervate the lateroventral somatic nerves. In *Oxyuris* the ventral ganglion is definitely paired, there being two groups of eight cells (31-38 r. l.) making a total of 16. The two extra ventral commissural cells of the nerve ring in this species probably correspond to two unipolar ventral ganglion cells in *Ascaris*; even so, only 18 ventral ganglion cells would have been accounted for and this is a marked reduction from 33. In *Cephalobellus* there are likewise eight pairs of cells but there is also a medioventral cell making 17 in all; one cell in each lobe is bipolar as in *Ascaris*. In *Spironoura* the partly bilobed ventral ganglion contains 29 neurones while in *Oesophagostomum* and *Rhabditis* 30 and 33 neurones were observed. In the latter instance the ventral ganglion is rather distinctly paired and also subdivided transversely into anterior and posterior lobes; each posterior lobe contains four cells (Fig. 131 Q).

Retrovesicular Ganglion. The retrovesicular ganglion in *Ascaris* contains 13 bipolar cells (79-91), several of which are in direct continuity with one another (Fig. 130 J) forming an associational center according to Goldschmidt (1908). In *Oxyuris*, Martini found the same number of cells in this ganglion as did the writers in *Cephalobellus*. In *Oesophagostomum* the retrovesicular ganglion consists of 13 cells (Fig. 132 A) followed so closely by a postretrovesicular ganglion of seven cells that sometimes they seem about to merge. This has apparently taken place in *Spironoura* where the retrovesicular ganglion is unusually far back and contains 20 cells. In *Rhabditis* the ganglia (Fig. 131 I) are also merged, there being 21 cells.

Anal, Lumbar and Genital Ganglia and Sensory Organs. In *Ascaris* these structures have not been very well studied though investigated by Hesse (1892), Voltzenlogel (1902) Goldschmidt (1903) and Deineka (1908). Each preanal genital papilla of the paired series is connected by means of a fiber (which passes through the hypodermis) to the ventrolateral nerve where a sensory neurone and a glia cell are situated. The fibers then pass posteriad in the ventrolateral nerve before reaching the genito-papillary commissures through which they reach the ventral nerve. (Fig. 128 C). The anal ganglion which terminates the ventral nerve contains seven cells; the number of cells in the lumbar ganglia has not been determined. According to Voltzenlogel the medioventral preanal papilla is innervated by a process direct from the anal ganglion, this process containing four neurones. On each side of this process a branch of the ventral nerve extends posteriad and just anterior to the anus both branches bend dorsally forming the *ano-lumbar* commissures which connect the ganglia of the same names. Voltzenlogel found that both the dorsal and medio-caudal nerves divide at the level of the lumbar ganglia, a process passing on each side to the corresponding lumbar ganglion. From these ganglia, the laterocaudal nerves extend posteriad. In all, there are seven pairs of postanal sensory organs in the male; the first four form two pairs of double subventral papillae, one pair anterior and one posterior to the lumbar ganglion. The fifth pair, more laterally situated and externally pore-like rather than papilloid, is the phasmid; the sixth and seventh pairs are both typical simple papillae. Anterior to the last pair the laterocaudal nerves each contain three neurones. All of the postanal sensory organs are innervated by processes from the laterocaudal nerves.

In *Ancylostoma* Looss found the anal ganglion longitudinally divided in both sexes. In the female the ano-lumbar commissures join the paired anal and lumbar ganglia from which ventrolateral caudal nerves extend posteriad to innervate the phasmids; just anterior to this point the dorsolateral nerves join the ventrolateral. In the male (Fig. 130 BB) the ganglia are essentially similar but the anal ganglia are each subdivided into two parts (antero-anal and postero-anal ganglia) and the lumbar ganglia each into three subdivisions (prolumbar, mesolumbar and metalumbar parts corresponding to lumbar, postlumbar and costal as named by Looss). Two ano-lumbar commissures join the subdivided anal ganglia with the two anterior subdivisions of the lumbar ganglia. In *Ancylostoma*, as in other strongyloids, all except one pair of genital papillae are situated in the bursa and terminate its rays. The prebursal papillae are the exceptions and they are innervated by processes extending directly from the second ano-lumbar commissure. The typical strongyloid (Fig. 33 I-J) bursal ray pattern consists of five bursal ray trunks, two ventral, two lateral and a single dorsal. Each ventral trunk bifurcates forming a ventroventral and a latero-ventral ray; each lateral trunk trifurcates forming an externolateral (ventrolateral), mediolateral and posterolateral (dorsolateral) ray while the dorsal gives off two lateral branches, the externodorsal rays, and then bifurcates, forming the two dorsal rays. Each of the dorsal rays terminates in two or three digitations. Since the dorsal trunk contains the remnants of the lateral and ventral chords as well as the somatic muscles, it corresponds to the tail of the female. It is not really dorsal, but terminal. Looss found that all the larger bursal rays terminate in papillae. The ventral trunks are innervated by a pair of nerves from the second ano-lumbar commissure; a branch from each nerve extends out to the tip of each ray. A nerve extends posteriad from each metalumbar ganglion and divides into three branches, one to each of the lateral rays, where they terminate as papillae, while another nerve extends medially from each metalumbar ganglion to the trunk of the dorsal ray, where it gives off a lateral branch into the externodorsal ray before terminating in the corresponding medial digitation of the dorsal ray. The papillae of the externolateral and externodorsal rays are situated on the dorsal side of the bursa while the remaining papillae protrude on the ventral side of the bursa. In both *Strongylus* (with tridigitate dorsal rays) and *Ocsophagostomum* (with bidigitate dorsal rays) we have found three pairs of papillae on each dorsal ray. There is a papilla for each digitation in the former genus while there is one papilla on each lateral and two on each medial branch in the latter genus (Fig. 132 N). With Looss, we conclude that in the male bursa the most medial digitation of the strongyloid dorsal ray is the homologue of the phasmid or "caudal papilla" of the female. Including the prebursal papillae there are 10 pairs of sensory organs in male strongyloids; this is also true for *Rhabditis strongyloides* (Fig. 4) *R. caussanelli* (Fig. 33 A) and *R. aspera* (Fig. 33 B-C). In *R. strongyloides* all sensory organs are papilloid while in *R. caussanelli* and *R. aspera* the tenth sensory organ (phasmid) is pore-like. Some of the genital papillae in rhabditids always end on the dorsal or outer side of the bursa; the particular ones vary with the species. In two or three species, such as *Rhabditis oxyuris* the first pair of papillae is prebursal as in the strongyloids. In order to find a comparable arrangement of bursal papillae in rhabditids we must number the strongyloid papillae from the anterior end as follows: prebursal—1, ventroventral—2, lateroventral—3, externolateral—4, mediolateral—5,

Fig. 132.

A-B—*Ocsophagostomum dentatum* (A—Dissection showing ventral and lateral ganglia with nerve trunks; B—Dissection showing dorsal and subdorsal ganglia). C-D—*Spironoura affine* (Reconstruction of posterior part of nervous system. C—Male; D—Female). E—*Rhabditis terricola* (Longitudinal section of female showing phasmidial gland). F-L—*Spironoura affine* (F—Longitudinal reconstruction of phasmids showing phasmidial glands, neurones and glia cells; G—Longitudinal section showing innervation of preanal median papilla; H—Same papilla in transverse section; I—Genital papilla; J—Deirid; K—Reconstruction of cross sections of female at level of phasmids; L—Reconstruction of cross sections of male showing spicular ganglia and rectal commissure). M—*Oxyuris equi* (Dissection showing connection of innervation processes with median nerves). N—*Oesophagostomum dentatum* (Branch of dorsal ray). M. after Martini, 1916, Ztschr. Wiss. Zool., v. 116. Remainder original.

posteriolateral—6, externodorsal—7, laterodorsal (digitation)—8, subdorsal (digitation)—9, dorsodorsal (digitation)—10 (= phasmid). Thus, the fourth and seventh papillae terminate on the dorsal side of the bursa. The similarly numbered papillae terminate dorsally in *Rhabditis strongyloides*; in addition the ninth (or tenth, depending on relative position) is also dorsal in this species; presumably it is the phasmid. The lumbar ganglia are not subdivided in rhabditids as they are in strongyloids.

In *Spironoura* the ventral ganglion is undivided and contains nine cells in the female (Fig. 132 D) and 27 in the male (Fig. 132 C). The lumbar ganglia contain six neurones on the right side and five on the left side; of these the first cell is somewhat removed from the remainder. The ano-lumbar commissures are approximately adanal in position connecting with the anterior part of the lumbar ganglia. From the posterior end of the lumbar ganglia the lateral caudal nerves extend posteriad and each contains a bipolar neurone before passing through the *phasmidial ganglion* from which fibers pass to the phasmidial gland. Posterior to this ganglion the lateral caudal nerves extend nearly to the caudal extremity. In the male of this form the ano-lumbar commissure is decidedly preanal and there is a medioventral process originating with it, containing a bipolar neurone connected with the medioventral preanal papilla (Fig. 132 G). Each prolumbar ganglion contains five neurones, one slightly anterior, which is connected with the recto-sympathetic system. In the course of the ventrolateral nerves anterior to the prolumbar ganglia, there are three neurones in each nerve from which a like number of nerve processes extend to the three pairs of preanal genital papillae. No genital commissures to the ventral nerve were observed, so we presume the axones of the three neurones pass posteriad and reach the ventral nerve through the ano-lumbar commissure. If this is the case, the distantly placed sensory cells might be regarded as part of the prolumbar ganglia. Postanally there are two pairs of nerve cell groups, the mesolumbar and metalumbar ganglia in addition to the phasmidial ganglia. Processes from the mesolumbars innervate the fourth to seventh pairs of genital papillae while processes from the metalumbars innervate the eighth to tenth pairs.

Regarding the general arrangement of genital papillae in nemas one's attention is called to two standard forms in the Phasmidia. In the first there is a very definite grouping of papillae as in strongyloids and rhabditoids; it probably reflects the triple division of the lumbar ganglia. Postanal papillae number up to seven or eight pairs including the phasmids. Preanal papillae number two to three pairs. In the second standard form the postanal papillae are not so clearly grouped and there are many more serially arranged preanal papillae, as in *Ascaris*; this linear formation is due to reduplication and probably arose from a form such as *Spironoura* in which the preanal papillary neurones are separated some distance from the prolumbar ganglion. The oxyurid-thelastomatid arrangement, in which there are but four pairs of papillae besides the phasmids, may be considered a reduction of the rhabditid scheme. A medio-ventral preanal papilla, innervated directly from the ventral nerve, was described in *Ascaris* and *Spironoura;* a comparable papilla is present in a large number of other phasmidian nemas and may even be general; one is recorded in *Strongyloides, Rhabditis, Physaloptera* and we have seen it in *Oesophagostomum*. The medioventral papilla of the preanal sucker in *Heterakis* (Fig. 33 P) might also be the same structure. We regard it as a probable homologue of the preanal supplementary organs (See p. 29) in aphasmidians.

PHASMIDS and ASSOCIATED STRUCTURES. Since our (1933) proposal of the divisions Phasmidia and Aphasmidia, parasitologists have been much perturbed by these "mysterious organs." They are nothing other than the "caudal papillae" as seen in the larvae and females of most parasitic nemas. Because of their differences from ordinary sensory papillae Cobb (1923) proposed the name phasmid (= ghost thing) for them. Their external manifestation is a pair of lateral or subventral pores. From each of these a short tube extends internally and in it lies the sensilla which is very similar to that of the amphid except that its elements or terminals are fewer in number. Like the amphids, the phasmids are usually (? always) provided with a flushing gland, the phasmidial gland. In the Phasmidia, our experience indicates that the phasmids are always present in larvae and females. They are sometimes transformed into plate-like scutella (*Rotylenchus blaberus* vide Steiner, 1937) and sometimes they take the form of large pockets as in larval dracunculoids and drilonematids (*Dicelis nira*). In the male, they are often difficult to distinguish from genital papillae or they may be so faint that they are truly ghost-like. In most rhabditids, cephalobids, diplogasterids, oxyurids and thelastomatids they are easily enough recognized and were called excretory glands by Stefanski (1922). In male spiruroids and dracunculoids they are very minute. Only in the males of a few rhabditids (*R. strongyloides*) and all strongylins are the phasmids grossly indistinguishable from genital papillae and we have seen (p. 169) that in these cases they are probably represented by the most posterior papilla or dorsodorsal digit of the dorsal ray. In *Oesophagostomum* it appears that this structure terminates in a pore as in typical phasmids.

The minute structure of these organs has been sorely neglected. Looss (1905) found them to be innervated by the lateral caudal nerves in *Aneylostoma*. Chitwood (1930) described the phasmidial gland and mentioned the observation of bipolar neurones ending in a sensory terminus within the phasmidial tube of *Rhabditis*, and the writers (1933) confirmed this finding in *Cephalobellus*. The illustration (Fig. 8) of the general situation in *Rhabditis terricola* is the only other information extant.

The writers have selected *Spironoura* for detailed study because it is optimum in size for histological work. Similar studies on free-living nemas are difficult; section and intravitam preparations, though beautiful, require confirmation because they are apt to be confusing. The errors of Deineka (1908) and Chitwood (1930) with methylene blue on the central nervous system make the description of an organ by section obligatory in at least one species before the use of intravitam staining methods for comparative purposes.

In the female of *Spironoura* each phasmid (Fig. 132 F & K) opens to the outside through a small postanal lateral phasmidial pore. From this pore a cuticularly lined canal extends inward and disappears in a large phasmidial gland. In the wall of the phasmidial canal there are two glia cells. The phasmidial ganglia each contains three neurones and one glia cell; processes from at least two of these enter the phasmidial gland where they form sensory terminals. The male has phasmids which are similar but the phasmidial ganglia each contains five neurones. In both sexes axones from these neurones pass anteriad through the lateral caudal nerves to the ano-lumbar commissures.

In rhabditids (Fig. 8 & 132 E) the phasmidial glands have the same general arrangement as in *Spironoura* but there is no separation between the lumbar and phasmidial ganglia.

RECTO-SYMPATHETIC SYSTEM. This part of the nervous system received casual attention by Hesse (1892) and Voltzenlogel (1902) in *Ascaris*, by Looss (1905) in *Aneylostoma duodenale*, by Martini (1906) in *Oxyuris equi*, and by the writers (1933) in *Cephalobellus papilliger*. Diagrams have, for the most part, been inadequate. Our observations on *Spironoura affine* indicate that there is probably considerable yet to be learned. The condition in the female of *Spironoura* seems to be quite simple (Fig. 132 D), since it apparently consists merely of a pair of commissures meeting dorsally and extending posteriad in the median caudal nerve. The latter contains two neurones dorsal to the rectum and two additional neurones in its postanal course. In the male of this form, the system is much more complex. In the course of each of the two ano-rectal commissures there are two bipolar neurones ventral to the cloaca (rc1-2 and rc3-4). As in the female, the commissures meet dorsally, forming the medial caudal nerve, but in its course there are three dorsocloacal neurones and four postanal neurones (Figs. 132 C & L). Laterally each ano-rectal commissure gives off a branch which joins the laterally situated *spicular ganglion* which contains four neurones and a glia cell. Two of these neurones have processes into the spicular sheath and two have processes to the medial caudal nerve (in the ano-rectal commissure). Two processes from each of these ganglia pass posteriorly and ventrally to two bipolar *subcloacal* neurones which extend toward the anterior cloacal lip.

An additional process connects the posterior part of the spicular ganglion to the ventrolateral nerve. In *Ascaris* Voltzenlogel found many errors in Hesse's description and diagrams of the male. Unfortunately no corrected diagram was supplied. We have attempted to make one on the basis of Voltzenlogel's description (Fig. 128 C) but it is necessarily liable to considerable error. According to the description each ano-rectal commissure contains two lateral bipolar neurones and the medial caudal nerve contains three dorso-cloacal neurones and one postanal neurone after which this nerve divides, sending a process to each lumbar ganglion. The two pairs of bipolar subcloacal neurones originate from the paired ventral nerve trunks and processes extend postcriad where a third subcloacal neurone is found. No spicular ganglia have been described. Despite the great detail

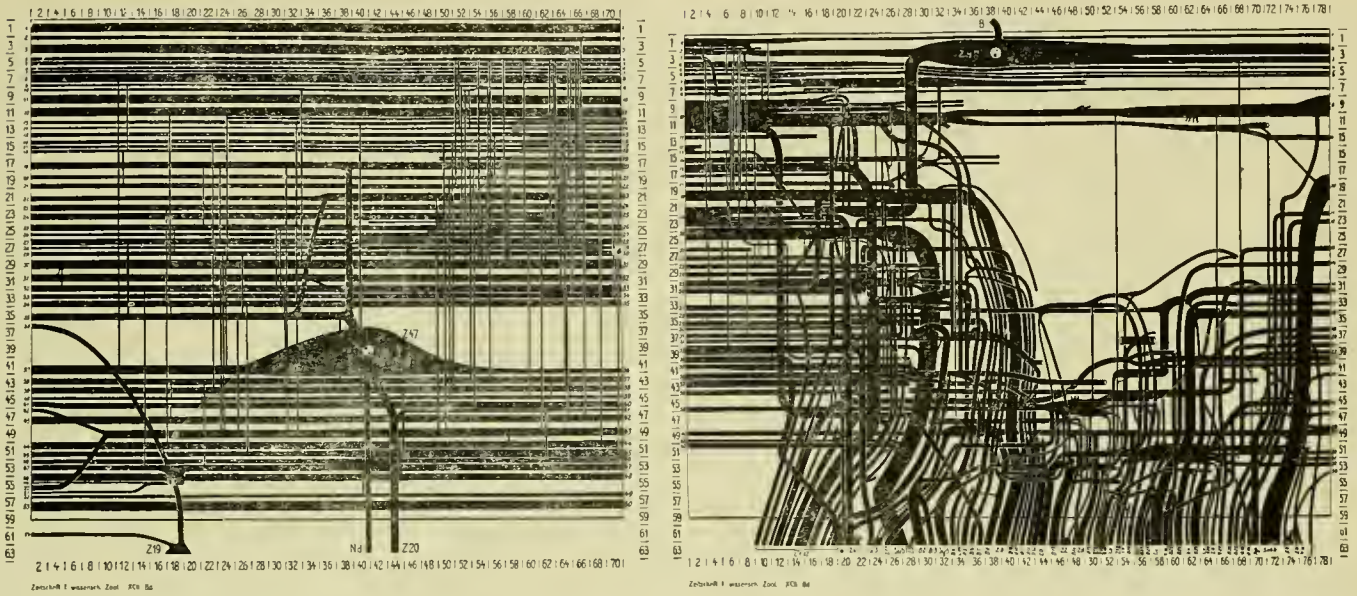

Fig. 133.

Diagrams of parts of nerve ring of *Ascaris lumbricoides*. Dorsal part of nerve ring on readers' left, ventral part on readers' right. See also fig. 130. After Goldschmidt, 1909, Ztschr. Wiss. Zool., v. 92 (2).

of Martini's work on *Oxyuris equi* we are unable to follow his description without diagrams. Looss is more intelligible and kindly supplies the needed diagrams but is not too exact. His findings in the female of *Ancylostoma* correspond with ours on *Spironoura* except that he found four neurones of the medial caudal nerve anterior to the anus. Two processes extend posteriad from the ends of the ventral nerve to the anterior anal lip. In the male the system consists of two commissures, one of which connects with the suprarectal ganglion, dorsal to the spicules, while the other connects with the subrectal ganglion, ventral to the spicules; the two ganglia are connected. The commissure connected with the suprarectal ganglion joins on each side with a subcloacal ganglion from which a group of fibers passes posteriorly to the dorsal side of the gubernaculum. There is obviously a distinct similarity in findings and differences between the conditions in *Ascaris*, *Spironoura* and *Ancylostoma* may be superficial and not important when an adequate amount of information for critical analysis is available.

Finer Structure of Nervous System

Work on the finer structure of the nervous system has been confined to *Ascaris lumbricoides*. Goldschmidt (1908) classified the nerve cells of this species as follows: I. Ganglion cells. Central cells (i. e. with one or rarely two processes to nerve ring) either (a) Direct or (b) Indirect (pass through a commissure before reaching nerve ring) and II. Sensory cells.

I. Central cells. The direct cells (Ia) were subdivided according to size and shape; large cells (Fig. 130) termed (1) *chonoid*, (Cell 23 Fig. V); (2) *corynoid*, (Cells 7-12, Fig. A); or (3) *amphoroid*, bipolar (Cells 19-20, Fig. B). Medium sized cells were classified as (4) *lagenoid* (Cell 26, Fig. D), (2) *corynoid* (Cell 18 Fig. A) or (5) *aranoid* (Cell 40, Fig. F). Small cells were classified as (6) *pyriform* (Cells, 1, 2, 4, Fig. A) or (2") *corynoid* (Cell 13, Fig. F). The Indirect cells (Ib) consist of large chonoid and small corynoid types.

II Sensory cells. These are bipolar cells situated either peripherically or centrally. They are of four general types according to disposition: (1) Direct sensory cells (Bipolar neurones of cephalic papillary nerves), (2) Indirect sensory cells (Bipolar neurones of amphidial nerves and genital papillae), (3) Collateral cells (Cells essentially bipolar but having one axone direct to nerve ring and a second axone passing through a commissure such as cell 39, innervating the deirid), (4) Unclassifiable bipolar neurones of longitudinal nerves such as those occurring in submedian and ventral somatic nerves (It seems dubious that these cells should be classified as sensory without knowledge of their ultimate destinations).

Supporting tissue. The supporting and ensheathing substance of the nervous system is called glia. Cells which form this connective tissue are of several types, some being very closely integrated into the general nervous system, the glia cells, others being less intimately associated. These latter include the *escort cells* (Geleitzellen) and the *clavate cells* (Kolbenzellen).

According to Goldschmidt (1910) the chief mass of glia which surrounds the nerve ring in *Ascaris* is two to three times as large as the nerve ring itself and contains nests of three to four small nuclei (Fig. 130 W). Some of the tissue and nuclei extend into the lateral chords. Special glia cells of the cephalic papillary nerves have already been described.

Each large ganglion cell has a specific glia hull surrounding it. According to Goldschmidt this material is often poorly fixed but in satisfactory preparations it may be seen that glia fibrils actually enter the ganglion cell (Fig. 130 V) thus causing the appearance characterized as "radially striated" ganglion cells. All nerve fibers have one or more neurofibrils and these are in direct continuity with the glia fibrils which may form a basketwork around the nucleus. The protoplasm of ganglion cells is essentially alveolar and the web conforms to the radial fibril structure. Tigroid substance (Nissl bodies, chromophil substance) is sometimes fine and generally distributed throughout the cell while at other times it is coarse and localized (Fig. 130 R-U).

Muscle Innervation. Due to the efforts of Schneider (1866) and later workers the nemic "innervation processes", by which somatic muscles are connected with longitudinal nerves, have received a great deal of publicity and it is widely accepted that nemas differ from

all other animals in that "The muscle seeks the nerve" rather than the reverse. The present writers frankly do not want to become involved in this controversial subject but will present as impartial a review of present day knowledge as is possible.

Technic has played a large part in earlier discussions and the two approaches to the subject have been via impregnation (silver method chiefly) or methylene blue, either as an intravitam stain or according to the ammonium molybdate technic. Apathy (1894) entered the field chiefly due to the taunts of Rohde (1894) whose studies of the muscle cells of *Ascaris* caused him to attack the whole structure of the school of neurone cytology which Apathy was developing. It was Rohde's dermis to the lateral chord but also becomes inserted into the cuticle. He did not differ with Apathy as to any facts, only interpretations. He viewed the entire fibrillar system not only within the muscle but also within the nerve cells as supportive. From his standpoint the entire theory that neurofibrils transmitted impulses was false. Invoking Koltzoff's Principle he explained the system as skeletal. According to this view nonspheroid cells develop an intracellular skeleton in order to retain their shape. Nerve cells are in direct protoplasmic continuity with one another (This cannot be denied at least as to some cells in nemas) and nerve impulses pass through the cytoplasm.

Such discussion is pure theory of broad application

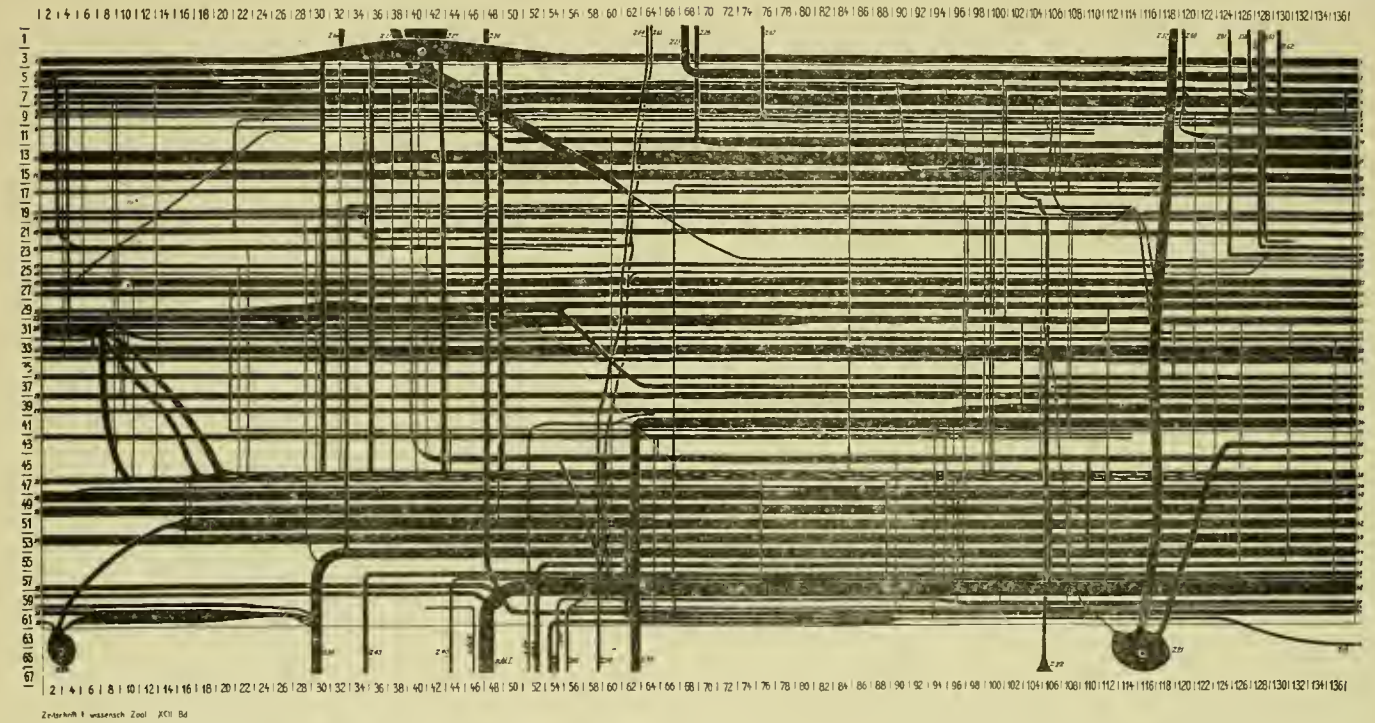

Fig. 134.

Diagram of lateral part of nervous system of *Ascaris lumbricoides*. Dorsal part of nerve ring on readers' left, ventral part on readers' right. See also fig. 130. After Goldschmidt, 1909, Ztschr. Wiss. Zool., v. 92 (2).

idea that the entire conception of the condition in other animals was fundamentally wrong and that the condition in *Ascaris* was typical. Apathy found the ascaridid muscle to contain an intimate and complex network of fibrils (Fig. 49 H) which not only converge in the "innervation" process but also continue into the hypodermis and finally reach the lateral and submedian somatic nerves. He conceived this "neurofibril" network as going from the median somatic nerve via the innervation process to the individual fibrils and thence back to the lateral nerves. Apathy explained the innervation process as an "interstitial muscle" in which a large neurofibrillar process was centrally located.

Deineka (1908), using intravitam methylene blue, observed direct union of nerve cells by contact and some intracellular neurofibrils passing from cell to cell. He described the "innervation" processes as direct branches of the somatic nerves each of which forms a wide terminal plate at its contact with the muscle (Fig. 130 X). As Rouville (1910-1911) and Goldschmidt (1910) pointed out this was a misinterpretation due to the stains flow along the process until it reached the chief part of the muscle cell. There can be no doubt that the innervation processes are directly continuous with the sarcoplasmic portion of the muscle cell.

Goldschmidt (1910) agreed with all the facts as presented by Apathy but pointed out that the central fibril of each innervation process is directly continuous (Fig. 130 Y) with a neurofibril and that the fibrillar network of the muscle cell not only passes through the hypo- and not particularly significant to nematology. No one denies that the fibrillar network exists and that neurofibrils pass *from the somatic nerves to the muscle cell* where they break up. Thus far nemas are in complete conformity with other groups of animals. The fact that the sarcoplasm of the muscle cell ensheaths the fibrils forming an "innervation process" no longer seems as important as Schneider and Rohde believed it to be.

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CHAPTER XII
NEMIC OVA

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Layers of the Egg Envelope

HISTORICAL REVIEW

R. O. C.

The history of the development of the egg of nematodes begins with the classic work of Nelson (1852) on *Toxocara cati*. Nelson recognized three portions of the genital tube set apart from each other by sphincters, namely: (1) the ovaries, (2) the oviducts, and (3) the uteri which join to form the vagina. He noted that the egg primordia of the extremities of the ovaries enlarged as they passed down the ducts forming the germinal vesicles at the center of which the nucleus or germinal spot was located. The yolk granules were considered to be derived either in the distal portion of the ovary or from the striated part of the ovarian wall near the junction of the oviduct. The vitellus was formed when the consolidation of the yolk was completed about the germinal vesicle.

According to Nelson the production of the vitelline membrane and the chitinous shell occurred in the oviducts. Following contact with the wedge-shaped sperm the eggs began to change in form. Almost immediately the chorion (chitinous shell) began to develop, three strata being recognized. The vitelline membrane separates off from the inner stratum when the chitinous shell is completed. Nelson implies that shell production is an endogenous process since there is no increase in total diameter of the egg during its development.

Bischoff (1855) criticizes Nelson regarding the penetration of the sperm, maintaining that he saw only epithelial cells adhering to the periphery of the vitellus. The diagrammatically clear descriptions of Nelson, however, and his excellent figures, leave no doubt that what he observed were actually the sperm-cells.

Meissner (1856) divided the genital tube of the Mermithoidea into four parts: (1) the ovary (Eierstock), (2) the vitellogene (Eiweissschlauch), (3) the tuba, and (4) the uterus. The vitellogene and tuba together correspond in part to the oviduct of Nelson. According to Meissner the eggs "ripened" in the ovary and during the process acquired a membrane which possessed a micropyle for the entrance of sperm. The egg was considered to be intimately related to the rachis as a sort of diverticulum which separated off as the eggs entered the vitellogene. In the vitellogene the chorion was first produced, and in the vaginal portion the protein coat was described as originating from a clear, droplet containing substance. The byssi, according to Meissner, are produced in the tuba. The uterus was considered to function only as a retention chamber for the eggs.

Küchenmeister (1857) described the formation of the chorion from a solidifying mass secreted by the walls of the uterus, laid down in constantly thickening layers about the vitelline membrane. Küchenmeister noted the difference between the appearance of the opercula and the chorion of *Trichuris*. In *Enterobius vermicularis* he described a light hood or cap at one end which he considered as an expression of the fact that the chorion had not been completed. This, in all probability, was the protein coat.

Cobbold (1864) describes the process of egg formation and membrane production in *Ascaris lumbricoides* essentially as does Nelson (*Loc. Cit.*). The ovarian portion he divided into the ovary and the vitellogene. The union of the sexual elements is immediately followed by the condensation of the yolk granules which obliterate the germinal vesicle. The ovum assumes an oval shape and the vitelline membrane and chorion form. The chorion finally assumes a regular tuberculated surface. In *Trichuris trichiura* he describes the abrupt termination of the poles at the end, and projection of a transparent inner membrane to form the opercular papillae.

Leuckart (1886) states that the eggs of *Ascaris lumbricoides* and *Trichuris trichiura* are thick-shelled, and the former further enveloped in an albuminous sheath usually colored with bile pigment. He describes the polar perforations in the latter species and notes that the opercula are albuminous plugs.

Blanchard (1889) describes the formation of two layers of the egg envelope after the egg reaches the uterus in *Ascaris*, the inner being more resistant to pressure and the outer more friable in spite of its great thickness. It is formed of concentric beds indicated by a delicate striation. The egg in the anterior (vaginal) part of the uterus comes into contact with a clear albuminous substance which is deposited over its surface. This substance is at first homogeneous but soon distributes in the form of small, hemispherical tubercles giving the characteristic appearance. The eggs are agglutinated together by their albuminous envelopes into a voluminous mass.

It thus becomes clear that some of the early workers recognized the three primary layers of the egg shell, namely: (1) the vitelline membrane, (2) the chitinous true shell, or chorion, and (3) the protein coat. The protein coat is generally accepted to originate from an exogenous process from the uterine secretion. The endogenous origin of the chitinous shell is implied by Nelson. Regarding the origin of the protein coat the general opinion is that it develops from a secretion of the uterus which adheres to the surface of the cuticular shell.

Ziegler (1895) noted that the eggs of *Diplogaster longicauda* and *Rhabditis terricola* entered the uterus and within an hour the shell is formed. In the former species he found no centrosome in unfertilized eggs and that the shell did not form. Rauther (1930) points out

that there is no specially modified structure for shell formation, and that it seemed probable that the chitinous shell was formed from a secretion of the egg itself.

Fauré-Fremiet (1913) reports on the endogenous development of the vitelline membrane of *Parascaris equorum*. He states that this membrane is formed from a particular fat body which pre-exists in the oocyte under the form of refringent bodies or crystalloids. He names the pre-existent substance extracted from whole gonads ascarylic acid.

Wharton (1915) gives the best description of the eggs of *Ascaris lumbricoides*. He describes the eggs as consisting of a central mass of protoplasm and yolk with a very thin vitelline membrane, surrounded by a thick, transparent shell consisting of an inner layer of chitin and an outer layer of some albuminous material. Like Blanchard (1889) he considered the chitinous shell to be composed of two parts, a thin, tough very refractive layer, and a thicker, more brittle outer layer which often showed delicate striations. The egg does not completely fill the shell, but forms a round ball in the center with a clear space at each end. The polar bodies were observed in this clear space. The pigmentation of the albuminous coat is considered to be due to the absorption of bile, a view held by Blanchard, since in females kept alive in Kronecker's solution the albuminous coat was colorless at the time of oviposition.

Thomas (1924) finds three principal membranes composing the envelope of eggs of *Trichosomoides crassicauda*; (1) the outer shell which stains black with Heidenhain's hematoxylin (protein coat), (2) an almost blue-gray fertilization membrane (chitinous shell), and (3) a brownish vitelline membrane. Between the vitelline membrane and the so-called fertilization membrane a peri-vitelline space is described.

Chitwood (1930), like Nelson (Loc. Cit.), considers that the eggs receive their shells while passing through the oviduct. He does not commit himself as to whether the development is exogenous or endogenous. In unpublished manuscript Chitwood points out that shell formation varies; in some species it occurs in the oviduct, whereas in others it occurs in the uterus. The production of the cuticular shell, he says, can be observed in the uterus of *Rhabditis terricola* if a mature female is isolated and observed for a few hours. The shell first appears as a delicate line which thickens as development progresses.

Wottge (1937) offers the most critical studies on the development of the eggs of *Parascaris equorum*. He found that following the penetration of the sperm a clear, transparent shell develops very quickly. This he called the homogeneous membrane. After its appearance the egg does not increase in size. The egg-cell itself shrinks in size and there is a corresponding reduction in the diameter of the homogeneous membrane. The first polar body is thrown off when this layer is completed. A second membrane then appears between the egg-cell and the homogeneous layer which is termed the striated membrane. It also develops rapidly, and is thick, with striations running parallel to its surface. After the production of this layer a wide space, the "Saftraum" or fluid cavity, develops around the egg-cell. When this is established the second polar body is discharged. These membranes remain unchanged during the further development of the egg.

From the above survey it is clear that the vitelline membrane is a zone of condensed protoplasm about the egg-cell (vitellus of Nelson) and that the chitinous shell forms rapidly about it. The diameter of the egg does not increase during shell production as it would if an exogenous process were involved. This was noted by both Nelson (1852) and Wottge. Both workers describe the peripheral protoplasm during shell formation as vacuolate and granular. A shrinking of the egg protoplasm away from the vitelline membrane leaves the peri-vitellus space or "Saftraum" of Wottge. The production of the shell in the Ascaridoidea is in the oviduct; in some other forms it may occur in the uterus. The protein coat forms by the adherence of the uterine secretion to the surface of the true chitinous shell. The brown pigmentation of ascarid eggs, and possibly others, is due to staining by the bile pigments. The so-called fertilization membrane of Thomas is undoubtedly the chitinous shell. The following section gives the sequence of development of the egg membranes.

LAYERS OF THE EGG MEMBRANE

R. O. C.

The present conception of the egg envelope is similar to the interpretation of Blanchard. Three coverings should be recognized, namely: (1) the protein external coat which is secreted by the uterine wall, (2) the chitinous membrane or true shell which is a secretory product of the egg itself, and (3) the vitelline membrane which is formed in the oviduct and binds the elements of the initial ovum together. In some groups, such as the Rhabditoidea, Tylenchoidea and Strongyloidea, the protein coat is absent in most of the species. It is also absent in ovoviviparous species such as *Trichinella spiralis, Dirofilaria immitis* and *Dracunculus medinensis*. In these forms a true egg of the strongyloid type is produced and hatching occurs *in utero*. All three membranes have been demonstrated in the Mermithoidea, Ascaridoidea, Oxyuroidea, Dioctophymatoidea, Spiruroidea, the oviparous Filaroidea, and some of the Strongyloidea. They are probably also present in some representatives of the Rhabditoidea, Plectoidea and Tripyloidea.

The protein external coat is variously modified in different forms. The terminal byssi described for the Mermithoidea (Figs. 139 & 140) are products of this layer and are continuous with the polar thickenings of it (Christie, 1937). Foster (1914) considers that the terminal filaments of the eggs of *Tetrameres sp.* are not simple prolongations of the chitinous shell but are added after the shell is complete. Our studies of the eggs of *Citellina marmotae* and *Tetrameres sp.* give the same impression. The opercula of the eggs of the Trichuroidea are protein akin but not identical chemically to the protein coat (Chitwood, 1938) and like the latter, the opercula might also be products of the uterine secretion.

The true shell presents little variation in morphology although it may be stratified in appearance. Biochemically the strata of the shell are the same notwithstanding the fact that Zawadowsky (1928) *et al*, divide the shell into three layers. The shell forms the general contours of the egg. In the Trichuroidea and Dioctophymatoidea it is discontinuous at the ends and projects collar-like parallel to the long axis forming the opercular aperture. Fig. 141Z shows a longitudinal section through the egg of *Capillaria aerophila* presenting the membrane relationships to the operecula. The shell is apparently formed of chitin (Chitwood, 1938) or a closely allied substance.

The vitelline membrane varies in its morphology in the different types. In some forms (*Toxascaris leonina, Toxocara vulpis* and *Parascaris equorum*) it is thick and filled with reticulations in the mature ova. In developing ova of *Parascaris equorum* the reticulations are not so apparent, but the peripheral zone is filled with granules similar to the so-called "secretory granules" of gland cells. The reticulations are apparently lipoidal since they, with other elements of the vitelline membrane, are dissolved in the ordinary fat solvents. Reticulation to a marked degree can be seen in the eggs of *Toxascaris*. Similar reticulations, though to a lesser degree, are present in the eggs of some of the Trichuroidea. In some species of parasitic roundworms the vitelline membrane appears as simply a wide zone of condensed protoplasm (*Enterobius vermicularis, et al.*), which is fairly resistant to mechanical abrasives. In others (*Necator americanus, et al*) it is a very delicate membrane which is scarcely discernible microscopically.

The sequence of development is as follows: The egg cells undergo a period of multiplication in the caecal or distal portion of the ovary. As they pass down the ovarian tube along the sides of the rachis each egg accumulates yolk material forming a vitellus. The vitellus is pyramidal in shape immediately prior to its discharge into the oviduct and contains a germinal condensation and a nucleus.

Upon reaching the oviduct the egg is fertilized and the vitellus begins to assume the subglobular shape typical of the species. This change of shape may be due, in part, to the contraction of the vitellus to form a sphere or it may result from the pressure exerted following the imbibition of water (Nelson, 1852). The shell begins to form immediately after the penetration of the vitellus by the sperm, and results from an endogenous process. This is evidenced by the appearance of


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Fig. 135.

glandular activity on the part of the periphery of the vitellus, granules similar to the secretory granules of gland cells being present and the protoplasm being extremely vacuolate. Even in the egg production of the trematodes in which specialized glands have been described presumably functioning in shell production there is evidence (Kouri and Nauss, 1938) that the shell is derived from the granules of the vitellus. Another point of evidence of endogenous development of the chitinous shell in the nematodes is the fact that after assuming a spherical shape the egg does not increase in diameter as it would with exogenous development. Figure 136 A shows the penetration of the vitellus by the wedge-shaped sperm, the condensed granular periphery and the vacuoles. The vitellus varies slightly from the typical pyramidal shape usually seen at this time.

The chitinous shell is almost completed by the time the egg reaches the uterus. The vitelline membrane has formed within the shell but does not show the degree of reticulation seen later. The protein coat is absent but begins to form as the egg enters the uterus. At first it is weakly mammillated and very thin. By the time of the discharge of the first polar body it is a well-established membrane. Figure 136B shows a uterine egg at the time of the completion of the protein coat. The vitelline membrane is diagrammatically represented in our figure, but can be seen at this time. The vitellus shrinks leaving a fluid cavity between it and the vitelline membrane, the "Saftraum" of Wottge (1938), or the peri-vitellus space. The tetrads of the first polar body can be seen, and the condensed chromatin of the male nucleus surrounded by the archoplasm. Figures 136C and D show two types of mitotic figures in the production of the first polar body. After division of the polar body the dyads are left as in figure 136E. A second polar body forms in the same manner. Figure 136F shows the completely developed egg with the male and female pronuclei. The two polar bodies can be seen, one against the vitelline membrane and the other in the vitellus which at this time is surrounded by a wide peri-vitellus zone. The vacuoles have disappeared.

Segmentation follows the release of the eggs from the host. The first segmentation stage results from the mitotic figure formed by the coalescence of male and female pronuclear material. Cleavage and embryology occur as shown for *Ascaris lumbricoides*, figures 137A to H.

The formation of the pattern of the protein coat of parasite eggs is difficult to hypothesize. Some workers describe molding chambers formed by constriction of the genital tube. They assume that the eggs pass along the duct single file and consequently the surface comes into contact with the epithelial walls. This may be true in some cases, but many of the most highly sculptored eggs occur in all levels of the uterus of some species in such numbers that their contact is problematical. This is certainly true in Ascaridoidea.

A more tenable theory of the development of the external sculptoring might be advanced on the basic precepts of colloidal behavior. The protein droplets in the uterus have a fairly high degree of consistency. As they come into contact with the shell they adhere at the point of contact. They congeal, possibly through loss of water absorbed by the vitellus, or possibly as a result of increase of hydrogen ion concentration in the neighborhood of the cell. Ascarid eggs have been shown by Nolf (1932) to require oxygen which results in the liberation of carbon dioxide as a waste. This might produce a pH differential between the uterine fluid and the periphery of the egg. If it is assumed that there is a specific difference in surface tension of the protein droplets, and the assumption seems reasonable, there would be a difference in size to the initial congealed particles. Subsequent addition of protein material would maintain the difference resulting in sculptoring of different degrees of prominence and different designs in the various species.

The production of specializations such as filaments and byssi are even more difficult to visualize. If a filament were present as a central cord they could be explained on the basis of adsorption phenomena but no such filament has as yet been demonstrated.

Unfertilized eggs possess no centrosome, have a granular appearing shell (Nelson) and a vitelline membrane. In some eggs the shell is reduced to a barely discernible membrane. The protoplasm is vacuolate from the time of the formation of the vitelline membrane until it degenerates. The protein coat may or may not be present (Fig. 135LL). In some cases at least, both the vitelline membrane and the true shell are apparently absent. In the parthenogenic species, *Rhabditis filiformis*, no vitelline membrane is formed in the developing eggs according to Chitwood (unpublished observation). The same appears to be the case in the parasitic generation of *Strongyloides ratti*, while a vitelline membrane is present in developing eggs of the bisexual free-living generation according to Chitwood and Graham (1940).

Fig. 135.

Nemic Ova. A-B—*Anaplectus granulosus* (A-ova, B-detail of shell, showing layers). C—*Rhabditis filiformis*. D—*Heterodera marioni*. E—*Rhabditis strongyloides*. F—*Heterodera marioni* (Stage similar to that named *Oxyuris incognita*). G—*Tylenchinema oscinellae* (Stylet in adult worm within second cuticle). H—*Mermis subnigrescens*. I—*Syphacea obvelata*. J—*Heteroxynema cucullatum*. K—*Oxyuronema atelophara*. L—*Travnema travnema*. M—*Enterobius vermicularis*. N—*Oxyuris equi*. O—*Passalurus ambiguus*. P-Q—*Protrellus aureus* (P—Cross section, Q—*longitudinal section*). R—*Pheudonymus sp.* S—*Dermatoxys veligera*. T—*Citellina marmotae*. U-V-W—*Ascaris lumbricoides*. X—*Parascaris equorum*. Y—*Toxascaris leonina*. Z—*Toxocara pteropodis*. AA—*Toxocara canis*. BB—*Aplectana gigantica*. CC—*Heterakis gallinae*. DD—*Oesophagostomum radiatum*. EE—*Ascaridia lineata*. FF—*Cyathostoma americanum*. GG—*Ancylostoma caninum*. HH—*Nematodirus filicolis*. II—*Necator americanus*. JJ—*Metastrongylus salmi*. KK—*Stephanurus dentatus*. LL—Ascarid eggs (1-2 fertilized, 3-10 unfertilized). A-E, P, Q, U and V, M, B, Chitwood. G, after Goodey, 1930. H, after Cobb, 1926. K, after Kreis 1932. L, after Pereira, 1938. Z, after Baylis, 1936. LL, after Otto, 1932. Remainder original, Christenson.

Abbreviations: *ml*, protein layer; *sh*, shell proper; *vit m*, vitelline membrane.

THE CHEMISTRY OF THE EGG MEMBRANES

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There has been much confusion concerning the number and kinds of membranes surrounding the developing nematode embryo in the egg. Zawadowsky and his collaborators (1914, 1928, 1929a, 1929b, 1929c) have written a number of papers describing the egg membranes of various species of *Ascarididae*, *Trichostrongylidae*, and of *Enterobius vermicularis* (*Oxyuridae*) and *Nematodirus spathiger* (*Trichostrongylidae*). In dealing with eggs of *Ascaris* and related species these authors speak of five membranes, an inner lipoidal layer, three middle layers which are designated *membrana lucida*, and an outer albuminous membrane which coats the egg; in dealing with the eggs of the other species they studied, they describe four membranes and homologize them with the membranes of ascarid eggs. Dinnik (1930), a worker in Zawadowsky's laboratory, figures four membranes, excluding the plugs, on the egg of *Trichuris trichiura*. On the other hand, Wottge (1937) and Chitwood (1938) could demonstrate chemically only three layers on the egg of *Ascaris lumbricoides*, and Jacobs and Jones (1939) found only three membranes on the egg of *Enterobius vermicularis* by means of similar chemical tests. Chitwood (1938) also described three membranes, excluding the plugs, on the eggs of *Dioctophyma renale*. It is difficult to interpret the homologies drawn by Zawadowsky and his co-workers relating the five membranes of the ascarid eggs to the four membranes they describe on the ova of the other species. Nevertheless, the fact that they designated the three middle layers of the *Ascaris* egg as *membrana lucida* and based their descriptions on the results produced with alcohol treatment and on the optical effects observed during the penetration of cedar oil into the egg, indicates the solution of the problem. The *membrana lucida* undoubtedly corresponds to the refractive part of the shell, which has been called the *homogeneous membrane* by Wottge, and the *shell proper* by Chitwood, and Jacobs and Jones. The latter have pointed out that the chitinous shell of *Enterobius* eggs is composed of two layers and that this layering is probably the reason Zawadowsky and his collaborators saw four different interfaces during the penetration of cedar oil into the pinworm egg. Biedermann (1912) has noted that the chitin found on various animal forms may be layered, and Schmidt (1936) has described different effects produced on plane polarized light by two layers of the chitin of *Parascaris equorum* eggs. The difference in the number of membranes described by various authors can therefore be attributed to the variety of techniques used in studying the eggs. Chemical tests show the presence of three chemically different membranes; physical tests detect the lamellation of these membranes.

The picture becomes clearer if the above interpretation is applied. The membrane immediately enclosing the embryo is the *vitelline membrane, fibrous membrane*, or *lipoidal layer(s)*. It corresponds to membranes "D" of Zawadowsky. The hard refractive membrane surrounding this is the *shell proper* or *homogeneous membrane*, corresponding to the *membrana lucida* (the middle layers) described by Zawadowsky. The outer covering is generally designated the *albuminous membrane;* it has been called the *proteinaceous membrane* by Jacobs and Jones. The latter is a more satisfactory term in view of its chemical nature, but for the sake of brevity it will hereafter be referred to as the *protein membrane.*

Ditylenchus dipsaci has been described by Chitwood as having only two membranes, the outer membrane being lacking.

Only a few authors have concerned themselves with the question of the origin of the various membranes. Fauré-Fremiet (1912a, 1912b, 1913) and Wottge (1937) have described the formation of the shell proper and the vitelline membrane following fertilization. Two consecutive series of vacuoles appear in the egg cell and move towards the surface. The first series transports glycogen to the surface where it is converted into glucosamine and finally laid down as chitin in the shell proper. The second series of vacuoles carries saponified lipoidal constituents of the ovum to the surface where they are transformed and deposited as the vitelline membrane. There is disagreement between the two workers (Wottge and Chitwood) who have studied the origin of the outermost protein membrane. Wottge, on the basis of the presence of this covering on unfertilized eggs, expresses the opinion that it originally exists as a sort of "ectoplasm" and is raised away from the egg by the secondary secretion of the other two membranes. The presence of rugose markings (*Ascaris*, etc.) and spirals (*Pseudonymus*) in the protein membrane could easily be explained by the assumption that regional secretion of the protein takes place on the surface of the egg cell. Chitwood, on the other hand, has found *Ascaris* eggs without this layer in the upper part of the uterus and with advancing stages in the deposition of this covering over the shell proper on eggs nearer the vagina. He suggests that the outermost membrane is a uterine secretion, added after the two inner membranes have been formed. Support for this view is found in the report of Wharton (1915) who obtained eggs without the protein membrane from female ascarids which oviposited for several days *in vitro* in Kronecker's solution. He attributed the absence of the membrane to "some physiological condition which prevents formation and deposition of the required substance by the uterine glands."

The outermost *protein membrane* generally exists as a coating around individual eggs. In some forms, however, it composes the matrix of the egg mass. Chitwood has described this condition in the egg masses of *Heterodera marioni* and the author has seen a somewhat similar condition in the eggs of *Enterobius vermicularis.* In the latter case the eggs are deposited in a mass in which the eggs are held together by the adhesive properties of the protein membrane, but they can be separated mechanically and each egg will retain its coat. The protein membrane has been studied chemically by Yoshida and Takano (1923), Wottge (1937), Chitwood (1938) and Jacobs and Jones (1939), on the eggs of *Ascaris, Dioctophyma, Heterodera*, and *Enterobius.* In all cases it has been shown to be a complex protein. It gives positive xanthoproteic, Millon's and ninhydrin reactions; is digested by artificial gastric and pancreatic juices; often swells and either wholly or partially dissolves in dilute mineral acids and alkalies, dilute acetic acid, and five percent NaOCl. Wottge assumes that some lipoidal material is present in this membrane on *Parascaris equorum* eggs because of the absorption of fat-soluble stains; Jacobs and Jones could not demonstrate lipoids in this layer on *Enterobius vermicularis* eggs. Chitwood obtained a positive Molisch reaction on an extract of the "gelatinous mass" of *Heterodera marioni* eggs and suggests the possibility that it is a glucoprotein. It may safely be assumed that there is variation in the composition of this membrane in the eggs of different forms, but that a fundamental protein base is present.

The *shell proper* is the first structure of the egg to have received attention. Apparently Krakow (1892) was the first to note the interesting fact that while the cuticle of nematodes is not chitin, their egg shells are composed of this substance. Early tests for chitin depended mainly on the insolubility of the substance in hot concentrated KOH. Fauré-Fremiet's descriptions of the origin of the shell proper indicate that he had chemical proof of its composition. Schulze (1924) apparently applied more specific tests in identifying chitin in the eggs of *Ascaris sp.* Later workers have made use of the van Wisselingh tests for chitin which are discussed by Kunike (1925) Kühnelt (1928) and Campbell (1929). The procedure is superheating the substance with concentrated KOH under pressure, any chitin being converted into chitosan by this process. Chitosan so produced turns brown on treatment with iodine-potassium iodide solution and then reddish-violet upon the addition of dilute sulphuric acid. It is soluble in dilute (3 percent) acetic acid and can by recrystallized from the acetic acid solution as minute sphaerocrystals by 1 percent sulphuric acid. It is soluble in 75 percent sulphuric acid from which it can be recrystallized by dilution. The sphaerocrystals thus produced are stained red by 0.1 percent Rose Bengal. These tests distinguish the substance as chitin; cellulose, the only other organic skeletal substance which will withstand the KOH treatment, does not stain with iodine-dilute acid, does not dissolve in dilute acetic acid, and does not yield the sphaerocrystals. Chitin is probably a general constituent of the egg shell throughout the class Nematoda.

Fauré-Fremiet, Wottge, Zawadowsky, Chitwood, and Jacobs and Jones have identified the innermost membrane as a sterol. The first two named authors are agreed that this membrane in *Ascaris* eggs is cholesterol. It is soluble in absolute alcohol, ether, chloroform, acetone, benzene, and xylene. It is not darkened by osmic acid, nor does it absorb fat-soluble stains such as Sudan III or Nile blue sulphate. It is dissolved slowly by saturated sodium sulphide and is insoluble in 10 percent NaOH, HCl, and acetic acid. It does not rotate the plane of polarized light. Wottge obtained a positive test for cholesterol on the membrane by the use of the Liebermann-Burchard reaction. In *Enterobius*, the solubilities of the membrane are the same as in *Ascaris.* According to Zawadowsky's results on the eggs of *Nematodirus spathiger* and of four species of *Trichostrongylidae*, the lipoidal membrane in these forms is slightly different in that it dissolves only partially in absolute alcohol and hardly dissolves in ether.

The knowledge of the chemistry of the egg membranes is of practical importance in relation to the control of nematode infections by destruction of the eggs. Early workers had repeatedly noted the difficulty of fixing nematode eggs even with the most rapid fixatives. Besides incidental studies on the permeability of the egg membranes to gases in relation to the requirements of development [Jammes and Martin (1907a, b; 1910), Fauré-Fremiet (1925), Szwejkowska (1928), Dyrdowska (1931)], Zawadowsky and his co-workers (1914, 1928, 1929a, b, c) and Wottge (1937) have attacked this problem directly. Their data allow the conclusion that although the membranes are very permeable to many gases, the vitelline membrane is semi-permeable to liquids and protects the embryo from damage by chemical agents; the protein membrane is an auxiliary chemical defense; and the shell proper serves as protection from mechanical forces. Huff (1936) has described a five-fold increase in oxygen consumption of developing *Ascaris* eggs after removal of the protein membrane. Wottge noted in his experiments that lipoid-dissolving substances did not penetrate to the vitelline membrane after the complete formation of the chitin shell. This difficulty of penetration was probably due not to the presence of the chitin but to the presence of the protein membrane which is to be found on eggs in that part of the uterus where eggs with well-developed shells are present. Jacobs and Jones have also pointed out that lipoid-dissolving substances can not reach the vitelline membrane until the protein membrane has been removed; if this outer coat is dissolved off, solutions can easily reach the vitelline membrane. They concluded that an effective ovicide must dissolve proteins and lipoids in order to reach the embryo. This statement should be modified to include substances which will dissolve or *be dissolved by* proteins and lipoids.

Recent work of Jones and Jacobs (1939) indicates that the protein membrane may also serve to inhibit desiccation of eggs subjected to unfavorable tempera-

tures and humidities. The hydrophilic properties of the protein allow the retention of moisture, and it is only after the membrane has been dried that desiccation of the embryo begins.

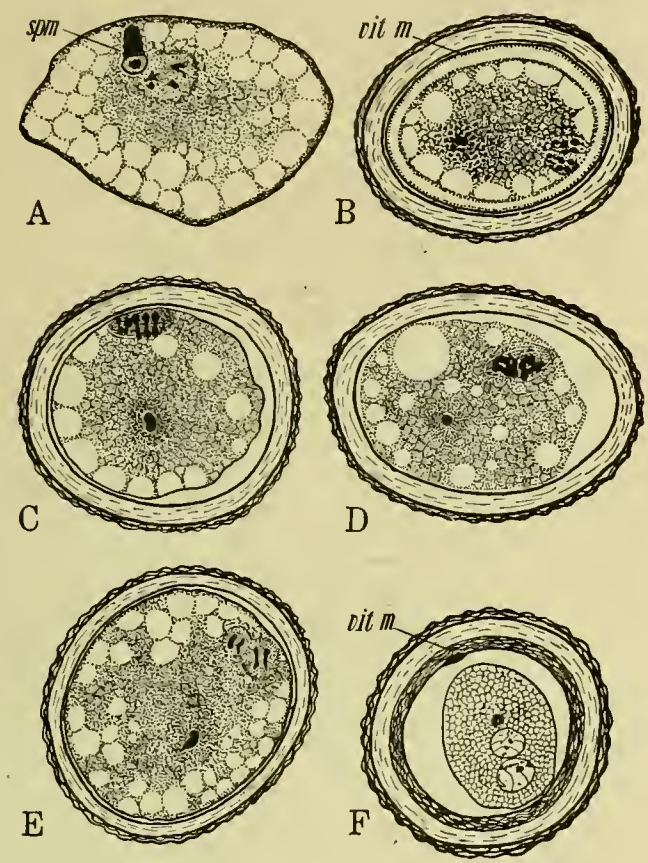

Figure 136.

A—The penetration of the sperm into the highly vacuolate vitellus of the egg. B—The tetrad of the first polar body. The shell and the vitelline membrane have completely formed. The vitellus has condensed toward the center of the egg leaving a space, the peri-vitellus space, between the vitellus and the vitelline membrane which is diagrammatically shown. The chromatin of the male nucleus is condensed and surrounded by granular archoplasm. C and D—The division of tetrads to form the first polar body. E—Dyads after the first polar body is given off. These divide to form the tetrads of the second polar body. F—The male and female pronuclei and the two polar bodies, the first against the vitelline membrane and the second in the vitellus itself. Fertilization (Fig. A) occurs in the oviduct. All subsequent stages are found *in utero*. Original, Christenson.

Abbreviations: *ml*, protein layer; *sh*, shell; *vit m*, vitelline membrane; *op*, operculum.
Original, Christenson.

Oviparity

R. O. C.

By far the majority of parasitic nematodes are oviparous. In some (*Trichuris trichiura, Ascaris lumbricoides, et al.*) the eggs are discharged in the unsegmented condition. After variable periods of incubation outside the host, usually of long duration, infective embryos are produced. Other species (*Necator americanus, et al.*) develop rapidly, hatching occurring in a few days. The liberated larvae undergo further development in the soil. In some species partial intra-uterine development of the larvae occurs. Typical morulae, for example, are produced in the eggs of *Contracaecum quadricuspe*, and *Habronema colaptes* before they are discharged (Walton, 1923). *In utero* development may progress until the eggs contain infective larvae in some forms. Such is the case with *Enterobius vermicularis* and many other species. Intermediate hosts are involved in the transfer of many nematodes, either the embryonated eggs or the infective larvae being taken up by annelid worms, arthropods and other essential hosts.

The condition of oviparity approximates ovoviviparity in some parasitic nematodes. Development progresses until larvae are produced and these hatch almost immediately after oviposition. This condition is seen in *Rhabdias bufonis*, a pulmonary parasite of Amphibia, or in *Rhabditella axei* (syn. *Rhabditis macrocerca*) as reported by Faust and Martinez (1933). After the discharge of the eggs in the lungs, in the case of the former species, they traverse the alimentary canal usually hatching in the rectal portion. Intra-host hatching likewise occurs in the case of *Strongyloides stercoralis* and *Spirocerca lupi* (*S. sanguinolenta*). Following gastric infections with the latter species the embryos are found free of the egg membranes in the caecum and colon of dogs. This parasite is likewise found commonly in aortic nodules from which the embryonated eggs are discharged directly into the blood stream where they hatch. The microfilaria-like, unsheathed larvae have often been confused with those of filarioid worms (Lewis, 1874, *et al*).

Ovoviviparity

R. O. C.

Ovoviviparity refers to the intra-uterine hatching of fully formed eggs. It is a wide-spread phenomenon among nematodes parasitic in tissues. Many of the so-called viviparous species are, in the strict sense of the term, actually ovoviviparous.

A good example of ovoviviparity is afforded by *Cosmocercella haberi*. In this species Steiner (1924) reports from one to three larvae, and one to five eggs in the uterus at one time. The case of *Trichinella spiralis* is complicated by a greater biotic potential but is none the less clear. Immature females possess typical eggs in the uterus, each composed of the segmenting protoplasmic mass, a vitelline membrane and a shell (Fig. 141AA). *Dirofilaria immitis* and *Dracunculus medinensis* are likewise commonly considered viviparous species which are actually ovoviviparous. In both cases typical eggs form which hatch *in utero* (Figs. 141 T & N).

Some of the other well-known, so-called viviparous forms should be included here. The eggs of *Onchocerca fasciata* are described by Badanine (1938), as covered by an excessively delicate membrane which may present either a spherical or oval outline. No attempt was made to determine the egg membranes present, but the figure given is fairly typical of the eggs of ovoviviparous species. Blacklock (1926, 1939) describes the eggs of *Onchocerca volvulus* stating that the egg membrane remained practically unstained when dried, fixed in alcohol and stained with hot haemalum. This procedure would destroy the delicate vitelline membrane leaving the shell which is undoubtedly the membrane Blacklock observed about the coiled embryos.

Augustine (1937) made some interesting observations of the early development stages of *Vagrifilaria columbigallinae*. He observed that the developing larvae in the uterus are enclosed in a delicate membrane but that no membranes were present about the larvae in the vaginal region. He found crumpled, hyaline objects in the vaginal part of the uterus which were similar in size and shape to the egg membranes indicating intra-uterine hatching.

Some authors go so far as to include under ovoviviparity species in which the embryonated eggs hatch outside the uterus. Kreis and Faust (1933), for example, consider *Rhabditella axei* (syn. *Rhabditis macrocera*), as being ovoviviparous but state that hatching occurs after the eggs have left the parent worm.

Whether or not viviparity in the true sense of the term actually exists in the Nematoda will have to be determined through critical research on early developmental stages of additional species.

Significance of the Embryonic Sheath

R. O. C.

Nematodes, like arthropods, grow through the process of ecdysis. Usually the cuticle is shed four times, the fifth stage thus formed being the adult. The so-called "infective stage" reached before the invasion of the definitive host in many species follows the second molt. This stage generally occurs in the soil (*Necator americanus, et al.*), or in an intermediate host. Molting usually follows shortly after the escape of the larvae from the egg envelope but it may occur in the egg itself. This

was observed by Seurat (1914) in *Nematodirus maurelanicus*. Cobb, Steiner and Christie (1923) show this to be the case in the development of *Agamermis decaudata*. It has also been reported for *Ascaris lumbricoides* v. *suum* by Alicata (1935), and in *Rhabdias fuscovenosa* var. *catanensis* by Chu (1936), and in other species. Some nematodes molt twice in the egg, two cuticles being present when the larvae hatch. In some instances the embryonic sheath is retained by the larvae as a loosely-fitting coat. This is especially true of the third stage, infective larvae of certain groups of the superfamily Strongyloidea, the second cuticle being the one retained. It is apparently protective in function. Occasionally the last two cuticles may be found covering the adult stage preparatory to the last molt. Goodey (1930) reports this to be true for *Tylenchinema oscinellae*, as shown in figure 135G.

In the Filarioidea the adult parasites live in locations often not associated with the natural openings of the body. Living young are discharged into the humoral elements. These may be sheathed (*Foleyella spp., Setaria spp., Isociella spp., Wuchereria bancrofti, Thamugadia hyalina, Saurositus agamae, Loa loa, et al*) or unsheathed (*Onchocerca spp., Dirofilaria spp., Dipetalonema spp., et al*). These larvae may live in the circulatory system for long periods of time without significant morphological changes, for example Underwood and Harwood (1939) transfused larvae of *Dirofilaria immitis* into uninfected dogs and found that they would survive over two years. Even unsheathed microfilariae can leave the blood stream and migrate through the tissues as has been demonstrated by Harwood (1932) in the case of *Litosomoides sigmodontis*.

Shortly after being taken up by the alternate host the sheath of unsheathed forms, such as *Wuchereria bancrofti*, is shed. Manson (1884) describes the process in detail as found in *Wuchereria bancrofti*, stating that it usually occurs within an hour in the mosquito vector. The shedding of the initial sheath in this species is followed by a striation of the larval integument. Yamada (1927) and Feng (1936) show that two additional molts follow

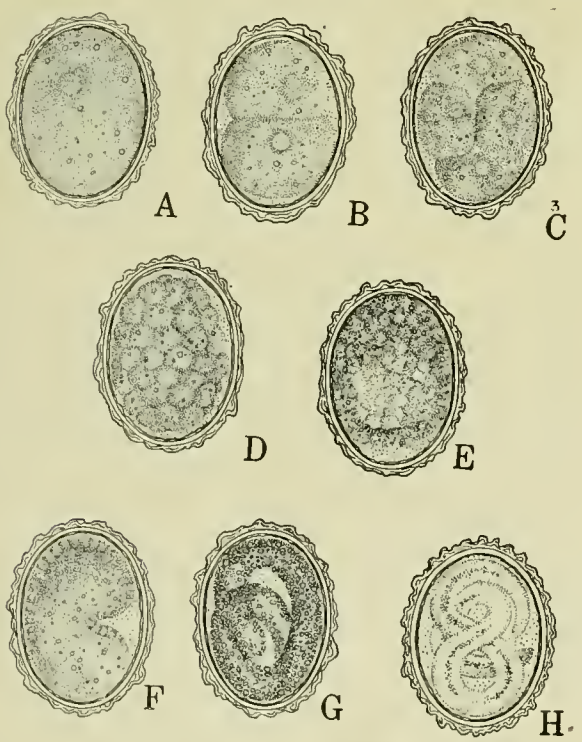

Figure 137.

Cleavage and early embryonic development of *Ascaris lumbricoides*. Figures A, B and C represent the 1-cell, 2-cell and 4-cell stages respectively. Figure D shows a late morula or early blastula. Figure E shows the cleavage cavity in a late blastula which is followed by gastrulation (Fig. F). Figures G and H give two stages in larval formation, the latter being the infective larva. Original, Christenson.

the initial shedding of the sheath. In unsheathed forms, for example *Dirofilaria immitis* and *Dracunculus medinensis*, only two molts occur in the vectors before the microfilariae are ready for their transfer. The first molt involving the initial sheath of *Mf. bancrofti*, followed by two additional, has led some workers to doubt that the first "cuticle" is homologous to the other two.

Penel (1904) advanced the idea that the initial sheath of *Loa loa* was derived from the vitelline membrane. He removed developmental stages from various levels of the uterus noting that the membrane enlarged with the growth of the larvae. In the vaginal portion of the uterus he recovered the sheathed microfilariae. His conclusion was that the larval investment was derived from the egg membrane. Penel's idea has been carried over to account for the origin of the sheath of *Mf. bancrofti* (See Fülleborn, 1928) and other species.

The modification of the egg membrane accompanying the development of the embryo has been seen in other species. Ransom (1904) shows that as the eggs of *Habronema muscae* develop the egg membrane follows the larval contours producing a sheath-like covering (Fig. 138). Faust (1928) notes a similar modification in *Thelazia callipaeda*. In the case of this species, however, there is a peculiar ballooning at the end, a large vesicle being formed. Faust states that the covering is retained for some time and that it is protective in function. Neither of these authors refer to a possible relationship between the modified egg membrane and the initial larval sheath. They, similarly, do not make a statement as to which of the egg membranes is involved.

Penel's idea that it is the vitelline membrane which forms the microfilarial sheath is not tenable. He, like most workers of his period, did not attempt a critical study of the membranes. Our studies show that the developing larvae of such so-called viviparous species as *Dirofilaria immitis* (Fig. 141T) and *Dracunculus medinensis* (Fig. 141N) are covered by a true shell within which there is a delicate vitelline membrane. This membrane is discernible only by careful study with oil immersion lenses in formalin-preserved materials. It is visible only at points of separation from the chitinous shell. Furthermore, Blacklock (1939) noted the presence of the egg membrane of *Onchocerca volvulus* following fixation in alcohol and staining with hot hemalum. It is safe to assume that the external membrane in this species, also, is the chitinous shell since the procedure used would destroy the delicate vitelline membrane. Augustine (1937) observed the shedding of the egg membranes in the uterus of *Vagrifilaria columbigallinae*, remnants of the shell being found in the vaginal portion.

It is thus clear that the chitinous shell is present in the eggs of ovoviviparous Filarioidea and Dracunculoidea which have been studied critically. The presence of a chitinous shell implies the presence of a vitelline membrane since the two appear almost simultaneously in the developing egg, and the early vitelline membrane must be considered to be simply the zone of shell formation (p. 175). That the chitinous shell has some elasticity and can adjust to the contours of the developing larva has been demonstrated by Penel, Ransom and Faust. This does not necessarily mean that the chitinous shell forms the initial microfilarial sheath. Biochemically the chitinous shell is not easy to distinguish from the embryonic cuticle (Chitwood, 1938) since both are highly insoluble. The critical test, solubility in hot alkalis, is often uncertain with such small materials.

Some workers express the view that the sheath of *Mf. bancrofti* is derived from the shed cuticle as is true of subsequent stages. As early as 1874, Lewis noted the presence of the sheath in *Mf. bancrofti* and its absence in *Mf. immitis*. He advanced two possibilities of formation, either it was derived as the shed cuticle, or it was derived from the egg envelope. More recently Augustine (1937) points out that in the fresh blood the sheath of *Mf. bancrofti* is extremely difficult to see, but that as heparinized blood dried the "formation" of the sheath could be followed. The efforts of the microfilariae to push on and back out caused a stretching of the once close-fitting, inconspicuous outer covering. He further states that it is quite possible that some stretching may occur in the circulation when the microfilariae are temporarily trapped in the capillaries. Augustine concludes that the sheath of *Mf. bancrofti* is comparable to that of infective hookworm larvae—namely, the result of an incomplete ecdysis. He advances the possibility that the

absence of the sheath in some species might be explained on the basis of delayed molting in which the formation of the membrane takes place in the vector.

The development of *Trichinella spiralis* should be considered briefly from the standpoint of sheath formation. Schwartz (1918) has demonstrated that trichinae removed from the alimentary canal of rats will undergo molting outside of the host. He does not state the number of molts undergone but implies that there are at least two before the adult stage is reached. So far as we are aware no one has attempted to determine the possibility of molting occurring before encapsulation of the larvae. Raffensperger (1918) found that trichina larvae were not infective 15, 17 and 18 days after infection, but were after 21 days. Our experiments showed that the point of infectivity was between 18 and 20 days. Nolf and Edney (1935) found the larvae infective after 17 days. Undoubtedly at this time some biological change occurs in the parasite, probably associated with molting, which results in their infectivity. The explanation of some workers that infectivity is the result of encapsulation will not hold since it is inconceivable that the connective tissue capsule, which is dissolved in the stomach, could offer any protection for the larvae against the stomach barrier. It is more probable that infectivity follows the second molt as is the general rule with other nematodes. The presence of the shed cuticles in the blood stream might be a contributory factor in producing the eosinophilia associated with trichina infection.

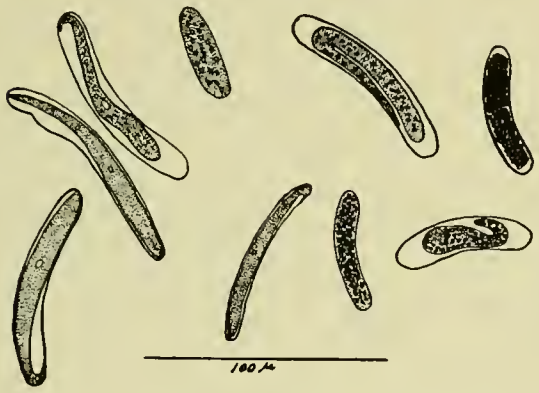

Fig. 138.

Eggs and embryos of *Habronema muscae*. After Ransom, 1913, U. S. D. A., B. A. I. Bull. No. 163.

Special Morphology

R. O. C.

Eggs of parasitic nematodes are variously modified to adapt them to ofttimes complicated life cycles. The more obvious of these specializations are the presence of byssi, terminal or polar filaments, equatorial filaments, opercula, and the mammillation of the shell. Byssi (Fig. 139) are branched, polar cords forming tassel-like structures on the eggs of the Mermithoidea. Apparently their function is to hold the eggs to the pubescent surfaces of plants until they are eaten by the essential hosts. Terminal filaments are found in certain genera of the superfamilies Spiruroidea and Oxyuroidea. They are unbranched structures which may occur singly, in pairs, or as tufts. These filaments may be unipolar or bipolar in distribution. Foster (1914) advances the idea that in *Tetrameres* (Fig. 141E) they function in holding the eggs together to insure massive infection of the hosts. Subpolar filaments are sometimes distributed over the surface of the egg accompanying the polar tufts. Equatorial filaments (Fig. 135R) occur in the genus *Pseudonymus* of the superfamily Oxyuroidea. They may function in the manner suggested by Foster for the filaments of *Tetrameres*. Chitwood (by correspondence) points out that species with filaments on the eggs are basically associated with an aquatic habitat, and that the filaments may function by entangling the egg in the vegetation thus preventing it from settling into the débris of the substratum which would reduce its chances of survival.

Among free living nemas hooks (*Anaplectus granulosus*) and minor excrescences (*Rhabditis filiformis, Mononchus punctatus, Trilobus pellucidus*) of the protein layer occur in some aquatic species. It is notable that *Rhabditis filiformis* is one of the very few species of aquatic *Rhabditis* and it is the only one known with a protein layer.

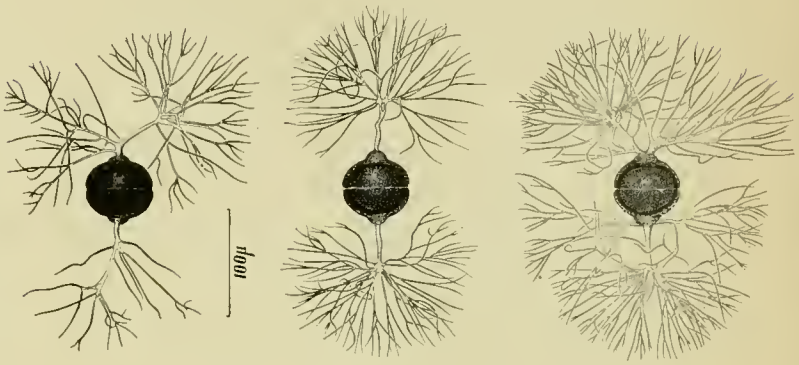

Fig. 139.

Eggs of *Mermis subnigrescens* showing variations in the form of the byssus. After Christie, 1937, J. Agric. Res., v. 55 (5) : 353-364.

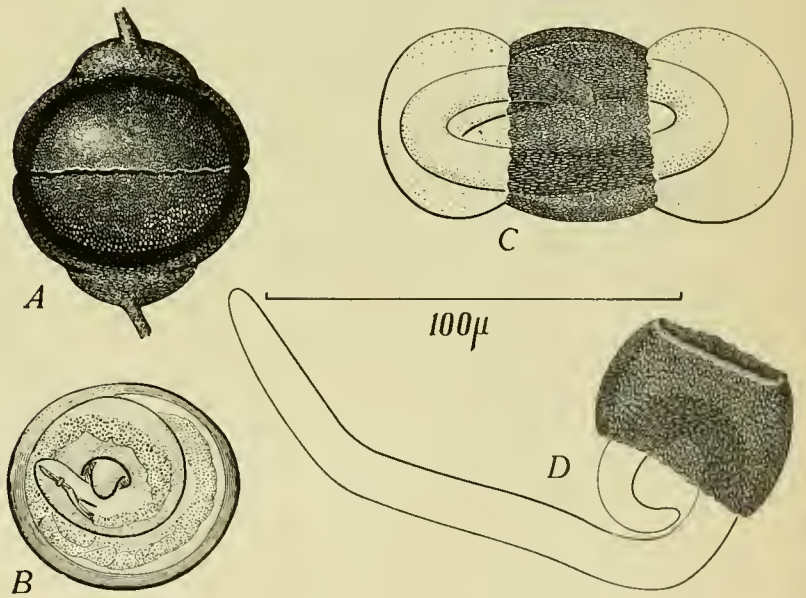

Fig. 140.

Egg of *Mermis subnigrescens*. A—showing outer and inner layers of shell; B—with outer layer of shell removed, showing larva within; C—in process of hatching; D—with larva emerging. After Christie, 1937, J. Agric. Res., v. 55 (5) : 353-364.

Opercula are zones of escape by which the embryos leave the egg membranes. They may have bipolar distribution and appear plug-like as seen in the Trichuroidea, and, to a lesser extent, in some of the other major groups. Some nemas possess a single operculum, others an opercular spot marked by the thinning of the membrane in a certain region, or the shell in some species may have lines of fracture indicating the area from which the embryo leaves the egg.

Mammillation, in the strict sense of the term, refers to the rounded excrescences over the surface of the

protein coat as seen in eggs of *Ascaris lumbricoides* (Fig. 135U-W) and *Dioctophyma renale* (Fig. 141BB-CC). Since there is a gradation between this type of external modification into pitting, ridging, and simple rugosity it seems proper to include all of these under a single general term. Mammillation, to some extent, occurs in most of the superfamilies of parasitic nematodes.

The foregoing specializations of the eggs will be considered in detail under the superfamily in which they are found.

EGGS OF FREE-LIVING NEMAS. M. B. CHITWOOD. Very little information is available regarding the eggs of free-living and plant parasitic nemas since they are seldom used as taxonomic characters. In the Rhabditoidea the eggs are usually of about the shape of the egg of *Rhabditis strongyloides* (Fig. 135E), both shell and vitelline membrane being simple and no protein layer being present. In a few species, however (*Diploscapter coronata, Rhabditis filiformis* and some cephalobids) the shell bears small protuberances (Fig. 135C) apparently formed by an exceedingly fine protein layer. In some parthenogenic species (*Strongyloides ratti* and *Rhabditis filiformis*) Chitwood and Graham (1940), found no vitelline membrane. In the Tylenchoidea, particularly the family Tylenchidae, there is quite a bit of variation in the relative length of the eggs, some species having short, thick eggs (*Aphelenchoides parietinus*), others rather narrow elongate eggs (*Heterodera marioni*, Fig. 115 M & Q, and *Aphelenchoides fragariae* Fig. 119E). *Heterodera marioni* is the only one of these producing a protein substance and this is produced in a mass rather than as an individual egg covering.

Eggs with protuberances or spines are also known to occur in a few species of free-living aphasmidians. These include *Anaplectus granulosus* (Fig. 120C), *Mononchus punctatus* according to Cobb (1917), and *Trilobus pellucidus* according to Steiner (1916). Some chromadorids have shells giving a punctate appearance. These species with modified egg shells are the only members of the Aphasmidia known to produce a protein layer. The eggs of few other nemas have been observed outside the parent so that, except for shape and relative size, little is known. In some forms such as *Chromadora sp.* (Fig. 120E) and *Microlaimus fluviatilis* the eggs are nearly spheroid while in others they are long and narrow as in *Achromadora minima*, described by Cobb, (1918), in which the mature egg is about one sixth the body length. All sizes and shapes between these extremes are known.

STRONGYLINA. (R. O. C.). Eggs usually with a thin, smooth shell, composed of two layers, the chitinous shell externally and the delicate vitelline membrane internally. In some forms a mammillated protein coat is present, for example *Metastrongylus salmi* (Fig. 135JJ). Usually there is a wide fluid cavity between the vitelline membrane and the cell mass. The shape is that of a regular ellipse in most species, but truncation has been reported for some eggs. While most of the ova measure below 100 microns, in the family Trichostrongylidae measurements approximating 300 microns have been reported. Operculation is a rare condition but has been reported. In most forms the ova are in early segmentation stages when discharged; embryonated eggs are rare. A few viviparous forms have been reported. A typical egg is that of *Necator americanus* (Fig. 135II).

Certain modifications of the egg envelopes occur in this group which deserve mention. Eggs of *Cyathostoma* possess an operculum at one pole as shown for *C. americanum* (Fig. 135FF). The chitinous shell of this species is relatively thick and truncated at one pole. Beyond it is a delicate extension enclosing a lenticular space. No line of fracture is evident microscopically but it is at this point the embryo leaves the egg envelope. The eggs are unembryonated *in utero*. Operculation has similarly been reported in other representatives of the family Syngamidae.

As in the case of *Cyathostoma americanum* the shape of strongyloid eggs often varies from the regular ellipse characteristic of most species. In *Nematodirus aspinosus* the egg is attenuated at one pole and truncate at the other; similar truncation exists in one pole of the egg of *Stephanurus dentatus* (Fig. 135KK). Eggs of *Nematodirus roscidus* possess a rugose or alveolate shell. A slight degree of striation appears in the shell of *Nematodirus fillicolis*. Some eggs are distinctly mammillated (*Metastrongylus salmi, et al*).

Eggs of the strongyloid worms are fairly uniformly below 100 microns in length. In three genera of the family Trichostrongylidae mammoth forms occur ranging upwards of 300 microns. The largest egg of which we have record is that of *Nematodirus orientianus* which ranges from 255 to 272 microns in length. The genera *Marshallagia, Nematodirus*, and *Nematodirella* all contain species with large eggs.

There is some variation in the degree of uterine development of the embryos in the superfamily *Strongyloidea*. The usual condition is that seen in eggs of *Necator americanus* (Fig. 135II), *Nematodirus fillicolis* (Fig. 135HH), or *Stephanurus dentatus* (Fig. 135KK), in which early segmentation stages are seen. In eggs of such forms as *Dictyocaulus filaria* and *Metastrongylus salmi* (Fig. 135JJ) intra-uterine development of the embryo occurs. Viviparity has been reported for the genus *Crenosoma* and a few other genera.

Figures 135DD and 135FF show the eggs of *Oesophagostomum radiatum* and *Cyathostoma americanum* respectively after incubation outside the host.

OXYUROIDEA. (R. O. C.). The eggs of the superfamily Oxyuroidea are usually described as possessing a double-contoured shell flattened on one side. The double-contoured appearance is due to the presence of the protein coat and the chitinous shell forming the external investment. Internally is the vitelline membrane of considerable thickness and durability in some species. In general the eggs are small but some species run above 100 microns in length, for example *Syphacea obvelata*. (Fig. 135 I). The eggs of some species possess polar filaments, equatorial filaments, opercula and mammillation of the shell.

Polar filaments are found in the eggs of *Citellina marmotae* and other species of the genus. Mantor (1930) describes the eggs of this species as thin-shelled, elongate oval in outline, and somewhat flattened on one side. From each pole there arises a long filament, broader at its base where it is attached to the outer shell and tapering to a fine thread. The filaments are equal in length and normally possessed by all eggs (Fig. 135T).

Peculiar equatorial filaments occur on the eggs of *Pseudonymus sp.*, a parasite of certain aquatic beetles. The normal number is two, but they may occur singly. They originate from a cone-like papilla on the protein coat and coil spring-like about the egg *in utero*. At oviposition the filaments unwind, rotating the egg on its long axis. The eggs are embryonated at the time of discharge (Fig. 135R).

Operculation is quite commonly seen in the Oxyuridae. Bipolar operculation is possessed by eggs of *Pharyngodon spinicauda*. The asymmetrical eggs of this species have prominent polar caps. In *Oxyuris equi* (Fig. 135N) a single operculum is present, the egg being somewhat similar to those of typical trematodes. The chitinous shell in this species is incomplete at one end, as is seen in the opercular apertures of the Trichuroidea, the end being closed by a thin, protein deposition. The egg of *Dermatoxys veligera* has a subpolar operculum marked by a prominent line of fracture (Fig. 135S). In the case of eggs of *Citellina marmotae* the operculum is likewise subterminal. The protein coat is evenly striated over its entire surface except at a point near one pole. Here the striation is lost and the membranes become thin. This marks the opercular spot described by Mantor (1930), appearing as shown in figure 135T.

Mature eggs of *Dermatoxys veligera* have excrescences over the surface giving the shell a striated appearance (Fig. 135 S). Freitas and Almeida (1936) describe two longitudinal ridges, which are strongly striated transversely, for the eggs of *Heteroxynema wernicki*. Chitwood (1932) describes a lateral crest on the flattened eggs of *Protrellus aureus* (Fig. 135P-Q).

Some workers lay much stress on the shape of the egg as a diagnostic character. The case which comes to mind is Kofoid and White's "*Oxyuris incognita*" which was described on the basis of asymmetrical eggs passed

by soldiers in Texas. The eggs seen (Kofoid and White, 1919) were of the flattened type usually possessing large, bluish-green globules at the end of the protoplasmic mass. Sandground (1923) pointed out that these eggs belonged to *Heterodera*, a group of plant inhabiting nematodes whose eggs will pass through the alimentary canal unaltered. Figure 135F shows the egg of *Heterodera marioni* which is similar to those found by Kofoid and White. These were extracted from worms occurring in nodules of potatoes. We have encountered similar eggs following gastric expression of a patient suffering chronic stomach trouble. A lettuce sandwich had been eaten shortly prior to the examination which was the cause of the so-called "nemic infection." Though often asymmetrical, the eggs of the Oxyuroidea may be oval as in *Oxyuronema atelophora* (Fig. 135K), spheroid as in some of the Thelostomatidae as reported by Chitwood (1932), or truncate as in *Oxyuris equi*.

The degree of development at the time of deposition shows considerable variation; *Oxyuronema atelophora* eggs are discharged in early segmentation stages, *Enterobius vermicularis*, and others, are embryonated at the time of discharge.

Zawadowsky and Schalimov (1929) figure the egg of *Enterobius vermicularis* as possessing a wide protein coat extending far beyond the chitinous shell. The appearance of the protoplasmic mass indicates that the egg figured was derived from the ovarian portion of the uterus. In all probability the "albuminous" coat had not condensed as it would later. Reardon (1938) shows the protein coat in this species to be much thinner at the time of oviposition, which is supported by our studies (Fig. 135M).

ASCARIDOIDEA. (R. O. C.). The eggs of the ascaroid worms have been studied by biologists since the middle of the past century. The classic work of Nelson (1852) demonstrating the penetration of the egg by the sperm and its subsequent development, and the cytological studies of Boveri (1888) have added much to our knowledge of the phenomena associated with sex cells. During more recent years studies on longevity, environmental factors influencing development, and on the permeability of the layers have been directed upon the eggs of this group. Ascarid eggs have become to cytology and cellular physiology what the frog is to general physiology and morphology, an indispensible laboratory subject.

In general the eggs of the Ascaridoidea are thick-shelled and possessed of three membranes in the egg envelope, namely: (1) the external protein coat which may be mammillated and deeply pigmented, giving a brown color; (2) the chitinous shell which is thick and quite transparent, and (3) the vitelline membrane which may contain coarse reticulation of the periphery. The typical shape is that of a regular ellipse but spherical or subglobular forms are well-known (*Toxocara canis*, Fig. 135AA). In some species the eggs are almost oblong in outline (*Ascaridia lincata*, Fig. 135EE). Usually development does not progress beyond early segmentation stages *in utero*, the eggs requiring relatively long periods of incubation in the soil before they become embryonated.

The protein coat of the ascaroid eggs is a thick layer in some species and coarsely mammillated, for example, *Ascaris lumbricoides* (Fig. 135W). In other forms it is thinner and marked by less prominent irregularities as seen in *Toxocara canis* (Fig. 135AA). Baylis (1936) describes the condition in *Toxocara pteropodis* as pitting (Fig. 135Z). *Parascaris equorum* has eggs in which the mammillations are even less pronounced. Upon surface view the exterior of the latter three species may give a honey-comb appearance. Other eggs present a perfectly smooth outline, the protein coat being barely discernible about the margin of the thick shell.

Variations occur in the appearance of the protein coat in normal eggs, but they are especially noticeable in unfertilized eggs. Unfertilized eggs of *Ascaris lumbricoides* have received much study because of their clinical importance (Miura and Nishiuchi, 1902; Foster, 1914; Otto, 1932; Keller, 1933; Matuda, 1939, *et. al*). In some instances the protein coat and the chitinous shell are apparently lacking, the vitelline membrane alone covering the highly vacuolated protoplasmic mass. In others the protein coat may be lacking, with the shell and the vitelline membrane appearing to be perfectly normal. In still other cases the protein coat may be thickened and distorted to produce grotesque shapes. Blanchard (1888) reports a stringy appearance in the mammillation occurring at times in normal fertilized eggs of *Ascaris lumbricoides*. This is thought to be due to the cohesion of eggs entering the vaginal portion of the uterus. Fig. 135 LL shows some of the variations found in unfertilized eggs of *Ascaris lumbricoides* as observed by Otto, 1932. Matuda (1939) points out that an anomalous condition is sometimes found in this species in which several egg-cells are bound together by a single chitinous shell. Stratification of the chitinous shell has been noted by some authors. Nelson (1852) observed this in *Toxocara cati*, and it has been reported more recently by Zawadowsky (1928) in several species of ascaroid worms.

The vitelline membrane is relatively thick and, in some species, filled with coarse reticulations. This is seen most clearly in the eggs of *Toxascaris leonina* (Fig. 135Y), but also occurs in *Parascaris equorum* (Fig. 135X). The reticulations disappear following treatment with ordinary fat solvents and are considered to be lipoidal in nature. The vitelline membranes in *Toxocara canis* and *Ascaridea lineata* have a dense, granulated appearance which may run toward reticulation.

Opercula have been reported for some of the ascaroid eggs. Dorman (1928) records two opercular plugs for the eggs of *Heterakis papillosa*. These, he states, are seen most prominently in the second membrane, but usually extend through all three. The eggs of *Heterakis gallinae* possess no plug-like structures but a lenticular clear space is present at one pole (Fig. 135CC). The shell may be somewhat thickened in this area.

Ackert (1931) presents a classic study on the morphology and development of the eggs of *Ascaridea lincata*. He states that the shells begin to form in the distal portion of the uterus, and that they are composed of three membranes: (1) an inner, highly permiable vitelline membrane, (2) the thick, resistant shell, and (3) a thin, "albuminous" covering. In one end a structure resembling a micropyle was seen which on micromanipulation was found to be a solid, conical appendage of the vitelline membrane. Baylis (1929) considered this structure to be an internal thickening of the shell.

Aside from the structures already mentioned the shell of Ascaridoidea eggs presents some additional modifications of interest. Olsen (1938) reports a thickening of one side of the shell in *Aplectana gigantica*. This egg is spherical, or subglobular in outline, and the thickening is confined to the chitinous shell and does not involve the other membranes (Fig. 135BB).

In general the eggs of the Ascarididae and Heterakidae require incubation outside the host before they are embryonated. There are exceptions to this, however, as in the case of *Ascaris phacochoeris* from the wart hog. Ortlepp (1939) finds intra-uterine development of the eggs to the embryonic stage in this species. *Cosmocercella haberi* is an example of an ovoviviparous form.

DRACUNCULOIDEA. R. O. C. But few observations have been made upon the intra-uterine stages of the Dracunculoidea. *Dracunculus medinensis*, a commonly reported viviparous species, is actually ovoviviparous since typical eggs are formed *in utero* covered by a vitelline membrane, a chitinous shell, and possibly a very thin protein coat presenting a slight degree of rugosity (Fig. 141N). Intra-uterine hatching occurs since the vaginal portion of the uterus is filled with the characteristic, long-tailed larvae.

True viviparity may occur in this group in the case of *Micropleura vivipara*. Baylis and Daubney (1922) state that the development of the embryos appears to be very rapid, the uterus being entirely filled, from end to end, with young apparently fully formed and not inclosed in membranes. Thomas (1929) similarly does not mention the presence of eggs in *Philometra nodulosa*. Van Cleave and Mueller (1934) likewise made no mention of the eggs in the latter species.

SPIRUROIDEA. (R. O. C.) Little can be said regarding the general characteristics of the eggs of the superfamily Spiruroidea. Usually they possess smooth, thick shells and are embryonated at the time of discharge. The egg envelope is composed of the three typical membranes; the protein coat, the chitinous true shell, and the vitelline membrane. The general shape is that of a regular ellipse, but various specialized shapes exist.

Fig. 141.

Nemic ova continued. A—*Mastophorus muris*. B—*Protospirura bonnei*. C—*Protaspirura numidica*. D—*Tetrameres* sp. from American woodcock. E—*Tetrameres nouveli*. F—*Cystidicola stigmatura*. G—*Hedruris siredonis*. H—*Metabronema magnum*. I—*Spiracerca lupi*. J—*Physocephalus sexalatus*. K—*Ascaraps strongylina*. L—*Oxyspirura mansoni*. M—*Rhabdochona avifilamenta* N—*Dracunculus medinensis*. O—*Gongylanema pulchrum*. P—*Physaloptera ortleppi*. Q — *Hamatospiculum cylindricum*.. R-S — *Hastaspiculum* sp. from *Erpetodryas fuscus*.. T — *Dirafilaria immitis* . U — *Diplotriaena tricuspis*. V — *Trichuris leporis*. W — *Trichuris trichiura*. X — *Trichuris vulpis*. Y — *Trichuris ovis*. Z—*Capillaria aerophila*. AA—*Trichinella spiralis*. BB-CC—*Diactaphyma renale* (BB-optical section, CC-surface). DD—*Sobaliphyme baturini*. EE—*Eustrongylides tubifex*. FF—*Eustrongylides elegans*. GG-HH—*Eustrongylides africanus* (GG-surface, HH-optical section). II—*Eustrongylides ignotus*. JJ—*Eustrongylides perpapillatus*. KK—*Hystrichis tricolor*. LL—*Hystrichis neglectus*. MM—*Hystrichis acanthocephalicus*. B, after Brumpt, 1931. E, after Seurat, 1914. G, after Chandler, 1919. H, after Yorke and Maplestone, 1926. M, after Weller, 1938. P, after Baylis, 1937. DD, after Petrov, 1930. EE-MM, after Jaegerskioeld, 1909. BB, CC original, Wallace. Remainder original, Christenson.

Terminal filaments, opercula, and mammillations have been reported in this group.

Terminal filaments have been observed in the genera *Tetrameres, Cystidicola, Metabronema, Ascarophis, Rhabdochona,* and *Spinitectus.* They are not uniformly present, however, in all species of the genera in which they occur. The number of filaments, and their length, is variable in some species while it is constant in others.

The filaments of *Tetrameres* were described by Seurat (1914) and Foster (1914). Seurat described an egg of the flattened oxyurid type possessing a tuft of filaments at each pole (Fig. 141E). He did not attempt an analysis of the membranes of the egg envelope. Foster noted similar filaments in a species of *Tetrameres* (*Tropidocerca*) from the American woodcock. He found seventeen to twenty-three filaments forming the polar tufts. Most of them were not over half the length of the egg, but one or two at each pole were twice as long (Fig. 141D). Foster points out that these filaments are not prolongations of the chitinous shell but are added after the shell is complete. He considers them analogous to the mammillations seen in the shell of *Ascaris lumbricoides,* a view which is supported by our studies. Sandground (1928) observed polar filaments on the eggs of *Tetrameres paucispina.*

Skinker (1931) gives a good discussion of the polar filaments that are found on the eggs of *Cystidicola stigmatura.* In no case were fewer than four present, and the majority of the eggs possessed from eight to twenty. The variable number, and differing length of these structures, is apparent from Skinker's figures. Not all members of the genus *Cystidicola* possess filaments, however, since Hunter and Bangham (1933) report their absence in *Cystidicola lepisostei.* Figure 141F shows the egg of *Cystidicola stigmatura* drawn from paratype material. The filaments, as in the case of *Tetrameres,* are derived from the protein coat. Van den Berghe (1935) observed both terminal and lateral filaments on *Cystidicola farionis.* They are similarly present over the surface of the egg of *Rhabdochona ovifilamenta* as well as occurring in polar tufts (Weller, 1938; Fig. 141M).

Van Beneden (1871) was the first to observe polar filaments in species of *Ascarophis.* He states that the eggs are distinguished from those of other nematodes by the presence of two filaments which garnish one of the poles. Nicoll (1907) likewise observed these structures. Cobb (1928) notes their absence in the uterine eggs of *Ascarophis helix.* Baylis (1933) includes them as a generic character in his recharacterization of the genus *Ascarophis* in spite of their apparent absence in the eggs of some species.

Polar filaments have likewise been observed in the genera *Spinitectus* and *Metabronema.* The condition in *Metabronema magnum* is worthy of mention since in this species two filaments arise from button-like opercula at each pole (Fig. 141H).

Operculation is a fairly common phenomenon among the eggs of the Spiruroidea. The button-like opercula of *Metabronema magnum* have already been mentioned. The eggs of *Hedruris siredonis* have opercula suggestive of the Trichuridae (Chandler, 1919). Baylis (1931) finds a similar condition in *Hedruris spinigera.* Some spiruroid eggs are truncate at both poles and the operecula demarcated by sub-terminal lines of fracture. Ransom (1904) reported this to be the case for *Oxyspirura mansoni* (Fig. 141L). It can be seen even more clearly in the eggs of *Ascarops strongylina* (Fig. 141K). In *Gongylonema pulchrum* the opercula are indicated by a thinning of the egg envelope with no lines of fracture being visible (Fig. 141O). Foster (1912) reports bipolar lines of fracture in the eggs of *Physocephalus sexalatus* (Fig. 141J) but they were not visible in our studies. The egg of this species is truncate at one end and possesses a lenticular operculum. The other end is somewhat attenuated and has a zone of separation between the chitinous shell and the protein coat. The area is not, however, suggestive of an operculum.

In the majority of the Spiruroidea the egg envelope is smooth and the contours regular, but mammillation and rugosity of the shell occur in the eggs of some species. Chandler (1919) reports the presence of two prominent, longitudinal ridges or "mammillae" running down the sides of the eggs of *Hedruris siredonis* (Fig. 141G). Mammillation in *Physaloptera ortleppi ortleppi* is expressed in the form of spinulation of the outer membrane. (Fig. 141P). The eggs of *Protospirura numidica* (Fig. 141C) are weakly mammillated, suggestive of the condition seen in certain well-known ascarid eggs, for example *Toxocara cati* or *Parascaris equorum.* A lesser degree of mammillation is seen in the rugosity of the shell of eggs of *Haplonema hamulatum.*

Brumpt (1931) shows a peculiar condition in the egg of *Protospirura bonnei.* These eggs are described as enclosed in a gelatinous sheath which sharply separates the egg from the surrounding débris. Apparently the sheath described is the slightly condensed uterine secretion forming a gelatinous protein coat similar to the condition found in many nematodes in the ovarian portion of the uterus. For example in the eggs of the filarioid worm *Hastospiculum sp.* from *Erpetodryas fuscus,* the eggs from the ovarian region of the uterus contain a slightly condensed, irregular protein coat (Fig. 141R-S) while those from the vaginal portion have the protein coat condensed as in the eggs of other species. It is conceivable that varying degrees of consolidation of the protein coat at oviposition are to be found among the different species of roundworms.

Filarioidea. (R. O. C.). Wide bionomic differences occur in the development of the Filarioidea. Many so-called viviparous species are known, some of which have been discussed in the section on ovoviviparity. The extent to which true viviparity occurs is a question which can be determined only on the basis of further research.

The eggs of ovoviviparous species are thin-shelled and contain usually but two membranes, the chitinous shell and the very delicate vitelline membrane. They usually have a smooth surface and are spheroid or ellipsoid in outline, as in *Dirofilaria immitis* (Fig. 141T), *Onchocerca fasciata* (Vide Badanine, 1938) or *Onchocerca volvulus* (Vide Blacklock, 1939). Intra-uterine shedding of the egg membranes has been observed by Augustine (1937) in the case of *Vagrifilaria columbigallinae,* and probably occurs in other species.

Oviparous species of Filarioidea are about equally as numerous as the ovoviviparous forms. The eggs are similar to those of the Spiruroidea in that they possess a protein coat, contain a coiled embryo at the time of discharge and are usually thick-shelled. As in the Spiruroidea considerable variation of morphology exists.

Baylis and Daubney (1922) describe the peculiar egg of *Hastospiculum macrophallos.* The eggs have a characteristic barrel shape, are thick-shelled and embryonated. Curious annular thickenings are present at each pole giving a superficial resemblance to the trichuroid type.

Chitwood (1932) describes the eggs of *Hastospiculum setiferum* as nearly spherical and embryonated *in utero. Hastospiculum onchocercum* has eggs of the same type with a "simple" shell. Chandler (1929) describes the eggs of *Hastospiculum spinigerum* as having a thick shell, further thickened into a collar near each end, the ends being covered by thin opercula; they contain developed embryos while still in the uteri. Figures 141R and S show the eggs of *Hastospiculum sp.* from *Erpetodryas fuscus.* Two different stages of intra-uterine development are seen. In Figure 141R the eggs were taken from the ovarian portion showing the partially condensed protein coat. The coat of the formed egg is seen in Figure 141 S.

Some genera apparently contain both oviparous and "viviparous" species. Walton (1929) describes two new species of the genus *Foleyella. Foleyella ranae* is reported as being viviparous, well developed embryos being present in the uterus. *Foleyella americanus* is implied to be oviparous since embryonated eggs are described as occurring in the lower uterine region. Similarly Walton (1935) noted eggs occurring in the uterus of *Isociella neglecta* whereas most of the members of the group have been considered to be viviparous. It is our opinion that in the case of both *Foleyella americanum* and *Isociella neglecta* that Walton's specimens were not entirely mature and both species are actually ovoviviparous.

Ransom (1904) describes the eggs of *Aprocta cylindrica* as elliptical and those of *Aprocta orbitalis* as thick-shelled, the mature eggs being embryonated. Caballero (1938) notes a double, thin shell for the oval eggs of *Aprocta travassosi.* The eggs of *Filaria martis* have been described as having remarkably thick shells with external shagreening.

TRICHUROIDEA. (R. O. C.). The eggs of the Trichuroidea possess three membranes; an outer protein coat which may be deeply pigmented presenting a brownish color; an intermediate true shell which is usually transparent, and an internal vitelline membrane which may be granular or possess reticulations (Fig. 141V). The most characteristic structures are the plug-like opercula at either pole. These penetrate the protein coat and the true shell, but not the vitelline membrane. In some species the opercula are very prominent, projecting well beyond the protein coat externally, and well into the egg cavity internally (*Trichuris ovis*, Fig. 141Y). In others they conform in length with the polar thickness of the egg envelope presenting even contours both externally and internally (*Trichuris vulpis*, Fig. 141X). The cuticular shell projects along the sides of the operecula forming collar-shaped sockets into which the opercula fit. The internal limits of the opercula widen beyond the diameter of the opercular apertures making them difficult to dislodge by mechanical means. Under pressure the egg-capsule itself will often break before the opercula are dislodged. The eggs are usually unsegmented at the time of discharge.

The appearance of the protein coat varies considerably. Thomas (1924) describes the eggs of *Trichosomoides crassicauda* as rugose. When the eggs of this species are discharged they are held together in stringy masses by a sticky secretion. This condition has also been reported by Walton (1923) for *Capillaria longistriata* and it occurs in the spiruroid genus *Gonglonema*. Pologentsev (1935) notes a striated appearance in the protein coat of ova of *Trichuris busulka*. A similar striation exists in *Capillaria aerophila* as shown by our studies (Christenson, 1935).

The eggs of *Capillaria magalhaesi* are described by Lent and Freitas (1937) as marked by circular and oblique striae. Baylis (1934) notes a punctate appearance of the shell of *Capillaria lophortygis*, and in *Capillaria brevicollis* and *Capillaria inequalis* it is mammillated (Walton, 1935). Faust and Martinez (1935) describe a striated or channeled sculptoring externally for the eggs of *Capillaria hepatica*.

Size has little diagnostic value in the ova of this group. Species of *Trichuris* give measurements which overlap and are therefore not significant (Chandler, 1930). The same is true for the genus *Capillaria*. It is of some value in separating species of Trichuroidea which may be present in a single host (Christenson, 1935).

Although usually considered viviparous our studies show that *Trichinella spiralis* is actually ovoviviparous. Immature females removed from the intestine of rats possess typical, thin-shelled eggs of the type shown in Figure 141 AA. The thin chitinous shell presents a slightly yellowish tinge and in spots the vitelline membrane was observed to have pulled away from it. Hatching occurs *in utero*, the minute larvae being discharged with no noticeable embryonic investments.

Figures 141V to AA show the eggs of some of the common trichuroid species occurring in man and domesticated animals.

MERMITHOIDEA. (R. O. C.). The bizarre eggs of the mermithoid worms have received much attention from biologists since they were first noted. Dujardin (1842) describes the eggs of *Mermis nigrescens* observing the peculiar, branched filaments termed byssi. (Fig. 139-140). Meissner (1856) further described the eggs of a form he considered to be the same species, noting their lenticular shape, the brownish color, and the two membranes composing the egg envelope enclosing a developed larva. He observed the transverse line of juncture of the outer shell, the polar thickenings, and the byssi arising from them as cords ending in tassel-like branches a short distance from the egg. He described the outer shell as essentially colorless, the brown color of the egg envelope being due to the pigmentation of the cuticular shell, or chorion.

Cobb (1926) expressed the view that the species studied by Meissner was not *Mermis nigrescens* of Dujardin but a different species which should be termed *Mermis meissneri*. He described a new species of *Mermis* under the name *M. subnigrescens* and presented an excellent figure of the egg (Fig. 135 H). He described the byssi as flexible, branched, entangling filaments which arise from polar elevations. He, also, noted the equatorial line of juncture between the two halves of the outer shell. Within the shell he shows the outline of the coiled larva with its three-pronged spear.

Christie (1937), like Meissner, observed the concentration of the pigment in the inner shell. This envelope is described as being spherical in outline and slightly compressed at the poles. No mention is made of the presence of a vitelline membrane but such a structure is shown in one of his figures (Fig. 139-140).

From the foregoing review it is apparent that the outer "shell" described by different authors is comparable to the protein coat, and that the byssi associated with it are not alien in origin to the terminal filaments of other forms. This view is supported by Meissner's description of the intra-uterine formation of the outer shell. The inner shell, or chorion, is the same as the chitinous shell of other groups, and that a vitelline membrane is present is indicated by Christie. Christie shows that hatching is accompanied by the fracture of the eggs at the polar thickenings (Fig. 140) similar to the condition reported by Ransom (1904) in the hatching of *Oxyspirura mansoni*, leaving the barrel-shaped shell remnants.

Some workers have been impressed with the similarity between the eggs of the Mermithoidea and those of the Trichuroidea. They point out that the thickened portion of the outer shell containing the byssi might be compared to the opercula in the latter group, and that in other details the eggs are similar. The analogy is even more apparent in non-byssate forms. Steiner (1938) states that the eggs of *Pseudomermis vanderlindei* are oval in shape, with heavy shells having both ends truncate, and containing fully developed embryos. He points out that they distantly resemble the eggs of the Trichuridae.

The lenticular shape assigned to eggs of some of the Mermithoidea is well seen in those of *Tetradonema plicans* as pointed out by Hungerford (1919). The eggs of this form are thick-shelled, somewhat testaceous in color, and disc-shaped in outline. When on edge an oblong contour is presented. These peculiar eggs are retained under the cuticula of the female after oviposition. All stages of embryonic development are seen *in utero*.

In some nematodes it has been observed that the first embryonic molt occurs within the egg envelope. This has been noted to be the case in the egg of *Agamermis decaudata* by Cobb, Steiner and Christie (1923).

DIOCTOPHYMATOIDEA. (F. G. WALLACE). The ova of the superfamily *Dioctophymatoidea* are unique among nematode ova in the form of the outer coat of the egg shell which is deeply pitted with funnel-shaped depressions. As representative of the group we may take the egg of *Dioctophyma renale*, which is symmetrically oval, 64 to 80 microns in length, and 36 to 48 microns in width (author's measurements). The shells of specimens dissected from the uterus of preserved forms are colorless, while those taken from urine-contaminated feces are brown. The surface of the shell is pitted with irregular-shaped depressions 4 to 7 microns each in greatest diameter. (Fig. 141BB-CC). The wall of each pit, when seen either in surface view or in optical section, appears to have a double contour. The surface of the shell between the pits is smooth. At either end of the egg, the shell bulges slightly, is free from pits, and is colorless. These clear ends are spoken of as terminal plugs.

The shell appears to consist of three layers; the external pitted coat or cortical layer, the inner shell, and the vitelline membrane. The terminal plugs though somewhat different in chemical composition, belong structurally to the outer coat. The entire shell measures 6.8 to 8 microns in thickness along the equator of the egg and reaches 12 microns in the terminal plugs. The greater part of this thickness (4.5 microns at the equator and 8 to 9 microns at the terminal plugs) is occupied by the cortical layer.

The studies of Chitwood (1938) and Lukasiak (1930) on the chemical composition of the various layers are in part inconclusive as formalin-preserved material was used, but it appears that the inner shell is probably chitinous. The terminal plugs differ from the rest of the cortical layer in being more soluble in KOH, sulphuric acid, sodium hypochlorite, and nitric acid. According to Balbiani (1870), whose figures of the egg have been copied directly or indirectly by most subsequent authors, the terminal plugs are the weakest points in the shell, as when embryonated eggs were subjected to cover-glass pressure the embryos escaped at the ends.

Table 2 gives the egg sizes taken from the literature and from the author's measurements of 50 eggs each from the uterus of a formalin-preserved specimen from a dog and from a formalin-preserved fecal sample from a mink.

Author	Length			Width		
	Min.	Max.	Av.	Min.	Max.	Av.
Present (dog)	72	80	76.7	40	48	44.9
Present (mink)	64	76	70.8	36	44	41.4
Balbiani (1870)			68			42
Blanchard (1889)	64	68		42	44	
Leuckart (1876)			64			44

Table 2. Ova of the Dioctophymatoidea. Egg measurements of *Dioctophyma renale* in microns.

The ova of the other genera of *Dioctophymatoidea*, namely *Eustrongylides*, *Hystrichis*, and *Soboliphyme*, all show considerable resemblance to the egg of *D. renale* in general size and in the pitted cortical layer. The drawings given by Jägerskiöld show clear terminal plugs for only a few species of [*E. africanus*, *E. ignotus*, *E. perpapillatus*, and *H. neglectus* (Fig. 141 EE-LL)]. The egg of *H. acanthocephalicus* differs from others of the group in having a network of ridges over the surface instead of the usual small pits (Fig. 141MM). The figures of the egg of *Soboliphyme baturini* Petrov show the pitted cortical and the inner layers of the shell (Fig. 141DD) but show in addition a structure not seen in the egg of *D. renale*, a plug at either end of the inner shell of such form that the egg, without the cortical layer, would resemble that of *Trichuris*.

Species	Author	Length		Width	
		Min.	Max.	Min.	Max.
Eustrongylides africanus	Jägerskiöld 1909	70	76	36	42
E. elegans	Jägerskiöld 1909	70	76	33	38
E. ignotus	Jägerskiöld 1909	58	66	35	44
E. perpapillatus	Jägerskiöld 1909	53	61	31	33
E. tubifex	Jägerskiöld 1909	65	75	37	44
Hystrichis acanthocephalicus	Jägerskiöld 1909	75	79	40	44
H. neglectus	Jägerskiöld 1909	71	74	41	44
H. tricolor	Jägerskiöld 1909	71	74	41	44
Soboliphyme baturini	Petrov 1930	80.6	89.9	43.4	46.5

Table 3. Ova of the Dioctophymatoidea. Egg measurements of the various species.

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CHAPTER XIII.

NEMIC RELATIONSHIPS

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Even to enter a discussion of nemic relationships invites criticism and focuses a spotlight on one's ignorance of zoology. It is difficult for a scientist to obtain sufficient knowledge to speak with accuracy concerning his specialty and whether or not he can do so outside his specialty remains to be seen. Undoubtedly there are as many separate theories as there will be readers of this chapter. Past and present theories, with their evidence will be presented. We hope and expect future workers will feel as much superior to us as we do to Bastian when we read "Having now pretty fully explained the anatomy of the Nematoids, we shall be able, with the aid of the many new facts revealed concerning their structure, to consider the question of their affinities and homologies with more chance of success than formerly, so that we may hope to throw some light upon this difficult subject."

Past Theories

TAXONOMIC ERA. The original relationships attributed to zoologic groups were based on casual knowledge of gross anatomy and were typically taxonomic in character. Thus Linnaeus (1758) divided the Animal Kingdom into six classes; Mammalia, Aves, Amphibia, Pisces, Insects, and Vermes. In the last mentioned group were included all the then known helminths as well as the Protozoa, Mollusca, and Annelida.

In 1800 Zeder established the groups of parasitic worms essentially as they are recognized today, the groups being Roundworms, Hooked-worms (spiny heads), Suckered worms, Flatworms, and Bladderworms; the same groups were named by Rudolphi (1808-09) Nematoidea, Acanthocephala, Trematoda, Cestoidea, and Cystica, all except the last of which have survived until the present time.

With the discovery in these animal groups of excretory and nervous systems, and with superficial knowledge of the body cavity and ontogeny, the classifications were expanded by Huxley and Haeckel who suggested approximately all of the possible relationships. Huxley's first classification (1856) divided the subkingdom into two phyla, Articulata and Annuloidea, the latter group including the classes Annelida, Echinodermata and Scolecida. The entire Entozoa, as well as the Rotifera and Turbellaria, were included in the Scolecida, thus the Entozoa would correspond to the term unsegmented worms in the broadest sense. The phylum Annuloidea was then characterized as having a water-vascular system. Shortly thereafter (1864) Huxley redivided and renamed his groups, characterizing the Annulosa as having a double chain of ventral ganglia and including therein the Arthropoda (= Articulata) and Annelida, leaving those without such a nervous system, Echinodermata and Scolecida, in the Annuloidea; he listed the classes Rotifera, Turbellaria, Trematoda, Taeniada (Cestoda), Nematoidea, Acanthocephala, and Gordiacea as comprising the Scolecida. On the basis of presence or absence of external ciliation he put forward, in 1878, the subdivisions Trichoscolecida for the first four classes and Nematoscolecida for the remaining classes plus the Gastrotricha *despite* ciliation in some members of the latter.

The most conspicuous feature in all discourses on nemic relationships from the time of Huxley to the present, is that the Nemathelminthes concept (including classes Nematoda, Acanthocephala, and Gordiacea or Nematomorpha) is not and never has been accepted by comparative anatomists though it is seemingly entrenched in zoologic literature.

Without attempting to go into detail, we shall outline the general theories with the points brought forward by the various authors, then give a comprehensive description of the primitive nematode, followed by an evaluation of the interrelationships of the various groups.

1. ECHINODERMATA-SCOLECIDA THEORY. This grouping, originating with Huxley (1856, -64, -78), received its only support from Bastian (1866) who saw the Nematoda as bridging the gap between the echinoderms on one side and through Acanthocephala to other scolecids on the other side. This theory was based entirely on the homology of the ambulacral and water-vascular systems. Though the ambulacral system opens on the dorsal side in many echinoderms (Holothuroidea and Crinoidea exceptional) and the water-vascular system on the same side in rotifers, the corresponding system opens on the ventral side of nematodes. Bastian states "for purposes of transcendental anatomy" it makes no difference which side is dorsal as long as the other organs (anus, reproductive openings) retain their relative positions.

2. ANNELID-CHAETOGNATH-NEMATHELMINTH THEORY. The earth-worm-ascarid comparison is by far the most natural since here two of the oldest known worms were originally considered congeneric and were subsequently separated. In 1866 Schneider classified all Vermes, as he knew them, on the basis of musculature. These groups were:

I. Nemathelminthes—skin and muscle tissue of body wall in two layers.

1. With one layer of longitudinal muscles, or two layers, the outer being circular and the inner longitudinal; lateral chords absent in latter.

(a) Unsegmented. Longitudinal muscles only.
Nematoidea
Chaetognatha

(b) Segmented

(1) Longitudinal fibres only, median chords only —Gymnotoma (for *Ramphogordius* "a segmented *Gordius*").

(2) Longitudinal and transverse fibres—Chaetopoda.

2. Inner longitudinal and outer circular muscles; lateral chords absent.
Acanthocephala
Gephyrea

II. Plathyhelminthes—Muscle fibres embedded in skin tissue, longitudinal, circular, and sagittal all one layer.

1. Oblique cross fibres absent.
Trematoda, Dendrocoela, Hirudinea, Onycophora.

2. Oblique cross fibres absent.
Cestoidea, Rhabdocoela.

As Schneider later (1873) stated, he viewed *Lumbricus* and *Nereis* as annulated ascarids just as he considered *Polygordius* an annulated *Gordius*. The idea of chaetognath-nemathelminth relationships has only persisted in a few of the more archaic textbooks and we understand the chaetognaths are now regarded by many workers as having lower chordate relationships. Bütschli (1875) pointed out that nematodes are embryologically unsegmented while *Sagitta* (Chaetognatha) is composed of three segments.

Vejdovsky (1886) proposed the group named Nematomorpha for the Gordiacea and the odd marine genus *Nectonema* and related the whole class to the annelids rather than to the nematodes. J. Thiel (1902) was particularly impressed by Nematomorpha-"annelid" relationships pointing out that the female solenogaster, *Neomenia*, has two posteriorly opening gonocoeles into which numerous germ sacs empty. Such relationship was apparently approved by Rauther (1909) who stated that the only similarity between nematodes and gordiids is that both are long thin worms. For the acanthocephalans Rauther suggested gephyrean relations dwelling to considerable extend upon *Sipunculus*. As will be seen later, Rauther viewed nematodes as primarily related to arthropods.

Greeff (1869) was so impressed by the secondary and superficial segmentation of *Desmoscolex* that he felt this

genus to be, indeed, the connecting link between annelids and nematodes and for many years the Desmoscolecidae were excluded from the Nematoda or considered an aberrant appendage. Not until Schepotieff (1908) studied the group and found its members to be internally of typical nemic structure, were the Desmoscolecidae accepted as part of the Nematoda.

3. Arthropod Theories. In reality there seem to be two schools of thought regarding nemic-arthropod relationships; the first school provides for the nematodes through degeneracy, the other through ascendancy, but at times the two theories seem to merge!

A. *Degeneracy.* Perrier (1897) seems to have originated the idea that free-living nematodes should be regarded as having originated secondarily from parasitic forms. The viewpoint was at that time more or less natural since the majority of zoologists were ignorant of free-living nematodes. Perrier's series Chitinophores, based on a "chitinous covering" and molts, included the Nemathelminthes with classes Nematoda, Acanthocephala and Gordiacea. This group was set entirely apart from the series Néphridés which included Rotatoria, Gastrotricha, Turbellaria, Trematoda and Cestoda.

Hubrecht (1904) followed with a theory in which it was plainly stated that free-living nematodes are much too "simple" to be archaic stem forms and must, instead, be secondarily degenerate products of the Arthropoda.

Rauther (1909) thereafter frankly invoked neoteny to explain all things in anatomy and relationship of worms. A direct quotation relating to possible gordiid-echinoderid relationship will serve best to illustrate this course of thought (p. 502). "der *Gordius*-Larve schreibe ich ebsowenig die bedeutung einer Rekapitulation einer primitiven Gordien-Stammform zu, wie ich in den äquivalenten Larven der höhern Würmer und Mollusken Abbilder von deren Vorfahren sehe. Die Auffassung der Echinoderiden als neotenischer Articulaten-Abkömmlinge wird ferner gerade durch ihre unzweifelhaften Aehnlichkeiten mit Nematoden gestützt (s.u.) welche letztern, wie sich im Verlauf dieser Ausführungen ergeben dürfte, selbst in analogem Verhältnis zu Articulaten-Vorfahren stehen." Further on, in the same publication he determined that the rotatorian is not a primitive form but the neotenic branch of a higher group reduced to the trochophore stage; that the nematode developed from a land-dwelling arthropod and that the search for ancestral groups is useless since they are phantoms.

Rauther's comparison of the triradiate pharynx of *Anopheles* larvae with the triradiate nematode esophagus and tardigrade pharynx is ingenious. He placed considerable weight on the stylet of tylenchids as compared to the paired stylets of tardigrades and dipterans; molting, rachis development of gonad, and rectal glands (as compared with malpighian tubules) were also cited as evidence of relationship. The Pentastomida (Linguatulida) were placed by Rauther as an intermediate group constituting a connecting link between nematodes and dipteran larvae.

Martini (1908) after previously (1903, 1907) establishing that meromyarian nematodes are ontogenetically primitive, switched to the view that the rhabditoid larva is an ontogenetic stage and *Rhabditis* is neotenic rather than primitive.

In the face of growing knowledge of free-living nematodes Keilin (1926) reiterated the "theory of degeneracy" without adding any new facts or thoughts.

This theory has cast its shadow over all nemic classification since it simplifies grouping so greatly. If, as Rauther suggests, ontogenetic stages are of no significance, then one may sidestep all difficult points. Concerning the invocation of neoteny to explain evolution within the Nematoda, Chitwood (1937) has stated, "Ontogeny supports the view that few-celled forms are more primitive than many celled forms. In the writer's opinion, the converse assumption removes the study of nemic phylogeny from the realm of logical thought."

B. Ascendancy. Those who have subscribed to the ascendancy idea have not necessarily believed that nematodes gave rise to arthropods but only that nematodes may be a branch coming off from the stock which eventually gave rise to insects or that free-living nemas developed from an insect-like ancestor and later gave rise to parasitic nemas. It should be noted that in no instance has an attempt been made by such observers to explain aquatic arthropods. Instead, it is apparently assumed that the Arthropoda must be a polyphyletic group.

Greeff (1869) being impressed with the secondary and superficial segmentation of marine nemas such as *Desmoscolex, Greeffiella,* and *Draconema* believed that these forms together with the Echinodera provided a connecting link between the Nematoda and the Arthropoda.

Bütschli (1876) supplied a much more substantial argument for common parentage of the two groups. As like characters he cited the absence of ciliation, occurrence of molting, presence of a nerve ring and ventral median nerve; he also homologized the trachea of insects with the lateral canals of nematodes and the nephridia of annelids. Bütschli further suggested that the caudal furcae of echinoderids may correspond to the arthropod foot and incidentally placed the Tardigrada as low arthropods. A diagram of the family tree, as he conceived it, is to be found in figure 146. Differences in the mode of jointing in arthropods and annelids, differences in cleavage and in the vascular systems caused him to separate them into two stem lines.

Ganin (1877) studied the nervous system of *Rhabditis* and because of the circum-esophageal commissure, double subventral nerve trunks and ventral chain of ganglia, he placed the Nematoda in the general arthropod series.

Maupas (1899) emphasized that nematodes molt in their life cycle as do arthropods and he even went so far as to compare the ontogeny of nemas with that of heteroceran lepidopterans in which four molts occur during larval development and two in adulthood. The encysted stage (ensheathed larva, resistant stage, dauer-larva) of nematodes and its ability to withstand adverse environmental conditions was compared with similar stages in tardigrades and rotatorians. However, Maupas could not accept rotatorian-nemic relationship because he was unable to find rotatorians molting.

Seurat (1920) presented by far the most comprehensive and well-founded arguments for common ancestry of nematodes and arthropods. First he defined the primitive nematode on the basis of habitat and comparative anatomy as follows: saprozoic, humid media, bilateral symmetry, mouth subterminal and ventral, three lips, tail thick and conical with three caudal glands, cuticle smooth, sensory papillae sparse, epidermis composed of four bands, four muscle fields, meromyarian, unicellular lateral glands. Mouth tubular, esophagus triradiate, and terminated by a valved bulb, intestine composed of few large cells, occasionally a caecum, rectum short with three glands. Excretory system with paired lateral canals opening laterally or without lateral canals but with a unicellular gland opening ventrally; sometimes with a secondary system opening posteriorly. Sexes separate, males with numerous genital papillae, two testes extending parallel anteriorly and opening posteriorly in a vas deferens and ejaculatory duct; a little anterior to anus large paired cement glands opening into ejaculatory duct; two spicules and a gubernaculum. Female with two parallel ovaries opening posteriorly through simple vagina, oocytes produced in small numbers. Segmentation total, unequal; four molts to adulthood.

Having stated his concept of the primitive nematode he recognized that such a form would combine characters of oxyurids and rhabditids. A common ancestral stem line with rotatorians and turbellarians would, according to Seurat's view, be eliminated due to the molts, chitinous cuticle, type of musculature, lack of cilia, form of gut, type of reproductive organs, and separation of sexes. All of these characters clearly point toward arthropods. The cuticular lining of the anterior arthropod gut and its differentiation posteriorly into a proventriculus, the existence of a caecum in the mid-gut (=chyliferous diverticulae), insignificance of hind gut, and the existence of malpighian tubules (as compared with anal glands) must (vide Seurat) be explained otherwise than by convergence with nematodes. The male reproductive system and spicules of nemas are compared with the testes

De Coninck (1938) has recently resurrected the term "Eutely" given by Martini (1923) to the phenomenon of cell constancy. He also made clear the distinction betwen this phenomenon and neoteny, attributing eutely to "very rapid segregation of all potentialities of the egg" while neoteny "is the result of hormonal deficiency". As to the distinction, the writers are in complete agreement.

and penis of insects. In the female each entire nemic ovary is compared to a single unit of the insect ovary; reduction in number of ovarian tubules is cited as evidence of relationship, such reduction having been reported by Cholodowsky (1908) in the dipteran, *Theria muscaria* Meig. Finally Seurat differed with Bütschli (1876) in that he homologized the lateral canals with the sericigenous glands of microgasters rather than with trachea. He pointed out the fallacy of Rauther's comparison of the triradiate pharynx of Anopheles larvae, Seurat's argument being that the three muscle bands or sectors extend from the *body wall* to the *external surface* of the pharynx and are hardly comparable to the radial muscles of nemic esophagi; rarity of the occurrence of a stylet in free-living nemas and its obviously secondary adaptive function in feeding were pointed out as evidence of the lack of phylogenetic significance of stylets. Seurat then asked, if in the presence of the evidence, one must not think of the primitive nematode as being a larva of the Holometabola adapted to detriticolous life, having lost all segmentation, become adult and sexual after having fulfilled its normal molts but preserving infantile characters. As a parallel instance of neoteny, the coleopterous malacoderm, *Phengodes*, according to Haase (1888), has a larval female possessing normally constituted genitalia and producing fertilized eggs. As contrary evidence Seurat cited the following differences between nematodes and insects: Absence in nematodes of any trace of segmentation or articulate appendages and anything corresponding to the trachea, as well as the divergence in cleavage of the egg. (The latter he felt could be explained through the presence of an abundance of yolk in the insect egg).

Baylis (1924) reviewed the theories extant and concluded that nemic-insect (arthropod) relationship is probable on the basis of the common cuticular esophageal (pharyngeal) lining, malpighian tubule-rectal gland homology, tubular form of gonads, homology of penis and spicules, metameric arrangement of setae in nematodes, common absence of cilia, paedogenesis of insect larvae, and molting. More recently (1938) Baylis expressed the view that the origin of nematodes is uncertain, perhaps in a very remote period nematodes and arthropods had a common ancestor but it would be unwise to press the suggestion since at the present time we do not know whether the conditions exhibited by dipterous larvae are primitive or secondarily adapted.

It will be seen from the above résumé that of all of the proponents of common nemic-arthropod relationships, Bütschli alone proposed a theory of descent presupposing direct rather than regressive evolution and he placed the Tardigrada as primitive arthropods. The majority of Seurat's points would be as acceptable to the concept of progressive as to the concept of regressive evolution. Paedogenesis might be even considered an atavistic tendency of insects. It would still be necessary to account for the origin of aquatic arthropods in order to accept progressive nemic-arthropod relationships but such an explanation is entirely unnecessary to the regressivists.

4. Scolecidan (Protonephridial) Theory. As previously noted, this theory is traceable directly to Huxley (1856) but it has undergone many modifications both by the original author (1864, 1878) and by other workers, the chief of whom was Bütschli (1876). This theory in substance, provides for the union of all "unsegmented worms" in one superphyletic group just above the coelenterates and ctenophores. All higher forms of life are supposed to have arisen from lower ancestral (primitive, extinct, rhabdocoele or rotatorian-like) scolecidans. Such a view presumes phylogenetic significance of the trochophore larva and is very close to the consensus of present day zoologic opinion. Disagreements relate to the subdivision of the "Scolecida" into its major series, phyla and classes.

Haeckel (1872, 1896) revised the Animal Kingdom on the basis of his "Gastraea Theory" placing the forms with neither body cavity nor anus in the Acoelomati; he accepted the common Platyhelminthes (renamed Platodes) grouping (Turbellaria, Trematoda, Cestoda) considering the platyhelminths as coelenterates and for them hypothesizing a simple gastrula-like ancestor with protonephridia. The Acoela were placed as the most primitive living worms and the Rhabdocoela as ancestors of all higher animals. Such an ancestral form is described as having two testes and two ovaries, a muscular stoma, no anus, a parenchymatous body cavity, an epithelial brain and an incompletely differentiated mesoderm. The formation of a body cavity, according to Haeckel, should be considered as a regression from a previously parenchymatous state. In his earlier revision (1872) he listed Rotatoria and Nematoda in the Coelomati. Later he revised this group into the "True Vermes" composed of the following phyla: 1. Rotatoria (with Gastrotricha as oldest and in turn descendent from Rhabdocoela). 2. Strongylaria (a) Echinocephala (=Echinodera, ancestral group, descendent in turn from Gastrotricha); (b) Nematoda (with gordiids as most primitive forms because of parenchyma); (c) Acanthocephala; (d) Chaetognatha. 3. Prosopygia (=Molluscoidea) and 4. Frontonia (=Nemertea). Rotatorian-like Trochozoa ancestors were assumed for the Molluscoidea, Nemertea, and Echinodermata, while annelids were derived from nemerteans. Arthropods were derived biphyletically from the Chaetopoda in two lines, —one the Crustacea, the other the Tracheata. Chordates were derived from trochophore-like ancestors in common with those which gave rise to the Nemertea. Pentastomes and tardigrades were both included in the Annelida.

Bütschli formed the group Nematorhyncha to include the Gastrotricha and Echinodera (Atricha); he related both of these groups to rotatorians on the basis that the somatic musculature in all three groups does not form a tube but consists of isolated cells extending through the body cavity as in a Pilidium. He also considered these forms as close to the ancestors of arthropods. Nematodes and nematorhynchs were closely associated with each other because of the superficial similarity of echinoderids to gordiid larvae, the similarity of the water vascular (excretory) systems of nematorhynchs and nematodes, and the similarity of the musculature of meromyarian nematodes to the musculature of gastrotrichs. Complete absence of circular muscles was pointed out as the chief factor separating rotatorian-nematode-nematorhynch series from annelid-gephyrean-platyhelminth series. The uniting of reproductive and digestive systems in male nematodes, in both sexes in gordiids, tardigrades and low arthropods he cited as evidence of their common ancestry. The excretory systems of platyhelminths, rotatorians, gastrotrichs and nematodes were considered undoubtedly homologous, while the tracheal system of insects and the metamerically segmented organs of annelids were considered divergent offshoots of the same system.

Stimulated by Gaffron's diagram of the nervous system of an ectoparasitic trematode, Bütschli (1885) compared it with that of a nematode and judged therefrom that a common ancestor must have existed. The dorsal brain and lateral nerves of the trematode need only to have bent ventrally forming a commissure in order to form a plan like that of a nematode. The lateral (amphidial) by-pass (lateroventral commissure) of nematodes preexists in trematodes.

Zelinka (1896) supported the opinion that gastrotrichs and rotatorians must have been derived from a trochophore ancestor and that echinoderids and nematodes probably arose from gastrotrichs.

Zacharias (1885) felt that he had established beyond doubt the common ancestry of nematodes and rotatorians on the basis of similar development (? bilateral cleavage).

Grobben (1910) crystallized the formation of a rotatorian-nematode group naming it the Aschelminthes and differentiating it from the Platyhelminthes on the basis of body cavity vs. parenchyma. In this group he included Rotatoria, Gastrotricha, Echinodera, Nematoda, Nematomorpha and Acanthocephala.

Martini (1913) considered the possible relationship of nematodes to both platyhelminths and arthopods and concluded that nematodes by possessing a hind gut are higher than platyhelminths, that the rectal glands of nematodes are homologues of tardigrade and insect malpighian tubules and that the excretory system of nemas might have had a separate origin and might not be homologous with that of platyhelminths.

Steiner (1919, 1920) subscribed to the general concept of Bütschli (1876) but was more explicit in the comparison of organs in nematodes and rotatorians. In general, it was his conception that nematodes developed from organisms similar to the philodinid rotatorians. He described the primitive nematode as a partially seden-

tary form with an H-shaped excretory system, valved esophageal bulb, caudal glands, and having vulva, anus, and excretory pore opening together (a separate orifice of the excretory pore somewhat posterior to the position in present day nematodes was considered as a possibility). He considered the mixture of radial and bilateral symmetry in nemas as due to their change from a mobile to a semi-sessile life. Bilaterality is associated with the mode of locomotion (dorso-ventral oscillation) of nematodes and radial symmetry with a sessile mode of life. Bilaterality occurs in the excretory system, musculature, and chords while radial symmetry occurs in the lips, mouth, and esophagus. As he conceived it, the appearance of radial symmetry coincided with the loss of cilia in the anterior part (corpus) of the esophagus and occurred when the original nematode was formed. This was a semi-sessile form. A plurality of present day free-living nematodes are partially sessile and when they move it is on the longitudinal axis; neither side is flattened for they do not normally rest in a prone position; in a dish of water they lie on their side abnormally. Apparently, he hypothesized, there was a primary motility, a secondary sessility (at origin of nematodes) and a tertiary remotility (within the Nematoda). Only this hypothesis could explain the mixtures of symmetries known to occur. Comparing the primitive nematode with the rotatorian he found it to conform in cuticle, hypodermis, presence of primary body cavity, divisions of gut (anterior, middle, and posterior), presence of caudal glands, original round form of body, and that possibly the musculature traces back to common ancestry. He considered the possibility of an homology of the dorsal side of the rotatorian with the ventral side of the nemic body, but rejected this hypothesis because of the embryology. The ventral side corresponds to the open side of the gastrula, identical in both groups. Measured from the posterior, the relative positions of the anus, reproductive and excretory system orifices are the same in the two groups; hence the orifice of the excretory system could first have separated from the cloace and thereafter the vulva of the female separated from the gut orifice. The variability in position of the vulva was cited as evidence of recentness of its separation. Paired parallel gonads were considered primitive for both sexes although no such example is known in free-living nemas. Ciliation of the anterior gut was considered primary; the mastax homologized with the esophageal bulb of *Rhabditis*, radial symmetry developing from bilateral. The amphids and accompanying glands were homologized with the retrocerebral organ and subcerebral glands of *Callidina*. On the whole, his comparison seems apt but the mastax is actually triradiate in symmetry, secondarily bilateral, and the ciliated anterior gut of rotatorians is a recent acquisition (secondary invagination), the primary stomodeum forming the mastax and esophagus (= esophago-intestinal valve of nemas).

More recently Remane (1928, 1929) has expressed the view that gastrotrichs are near the ancestor of both nematodes and echinoderids and that they in turn developed from archiannelid-like (trochophore) progenitors. A trochophore origin was also suggested for rotatorians but the unsuitability of the Trochhelminthes (Zelinka included rotatorians, gastrotrichs and echinoderids) as a systematic group was pointed out. Rotatorians differ from gastrotrichs and echinoderids, as well as from nematodes, by having circular muscles, a ciliated foregut, and bilateral mastax all of which are secondary developments. Remane subscribed to the Aschelminthes concept.

The Primitive Nema

Having brought forward the various theories to account for nemic origin we need examine them in the light of present knowledge. In order to do this a picture should be formed of the primitive nema. Considering the various types of evidence customarily available we find some forms of knowledge conspicuous by their absence, others by their richness.

Geology. Taylor (1935) reviewed the knowledge of fossil nemas and listed a total of six species of which two were mermithids while the remainder were free-living nemas. The mermithids [*Heydonius antiquus* (v. Heydon, 1862) and *H. matutinus* (Menge, 1866)] were collected from Rhine lignite (Eocene) and Baltic amber and the free-living nemas [*Oligoplectus succini* (v. Duisburg, 1862), *Vetus duisburgi* Taylor 1935, *V. pristinus* (Menge, 1866) and *V. capillaceus* (Menge, 1866)] were all found in Baltic amber (lower Oligocene). As no morphologic details can be distinguished the records are of no advantage from that standpoint; neither are they of value in determining the origin of nemas since the group obviously must predate the Tertiary. These records, however, help us to understand why fossil nemas are so rare. The nema has no hard parts such as insects have for preservation and a nema must be included in a deposit such as rosin or something of exceedingly fine grain. Repeated examinations of fossil shales and ambers by the writer have been uniformly negative.

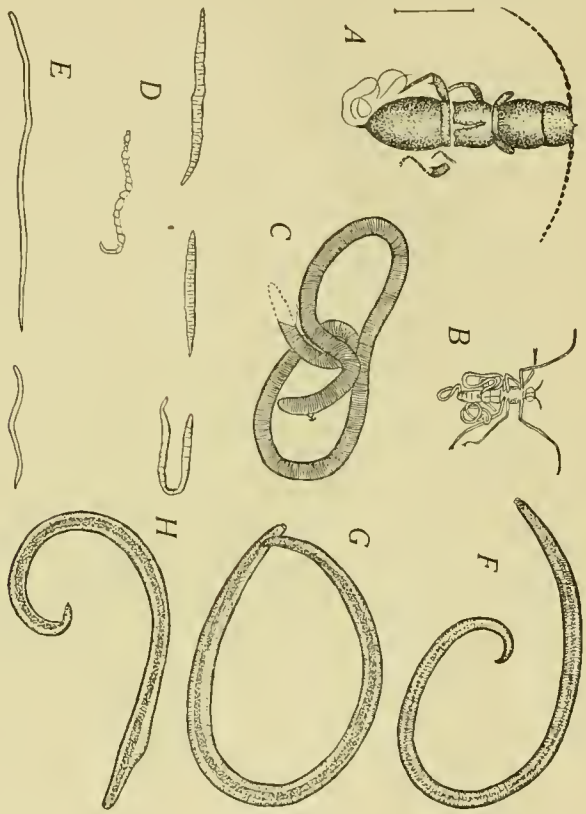

Fig. 142.

Fossil nemas. A—*Heydonius antiquus;* B-C—*Heydonius matutinus;* D—*Vetus pristinus;* E—*Vetus capillaceus;* F—*Oligoplectus succini;* G-H—*Vetus duisburgi.* After Taylor, 1935, Proc. Helm. Soc. Wash. v. 2 (1).

Distribution. Among the free-living nemas there seems to be little correlation between geographical locality and species. Both saprozoic and predatory forms are more specialized as to medium than continent. In some freshwater groups Thorne (1929) has found European species common on the western mountain peaks in this country, while those associated with decay may be considered universal. Identical marine species have likewise been collected from European and American Atlantic coasts though this parallel occurrence is less common. Genera among free-living nemas are certainly worldwide. In parasitic nemas, the parasites distribution is usually coincident with that of the host.

The parasites of man have received considerable attention from the standpoint of distribution. The "American" hookworm, *Necator americanus*, is distributed over a large part of the earth and it could easily have been imported to the Americas with negroes from Africa (Fig. 143). Two filariids of man, *Wuchereria bancrofti* and *Dipetalonema perstans* (syn. *Acanthocheilonema perstans*) seem to have originated in Europe or Asia and later to have been brought to the Western World (Fig. 144).

Evidence of the origin of physiological races of a species in two or more hosts (ex. *Ascaris lumbricoides* in pig and man) may indicate at least one line of evolution.

As yet there seems to be too little information about such races among either parasites of animals or plants for any conclusions to be drawn.

Steiner (1917) discussed the habitat distribution of free-living nemas, pointing out that there are two chief faunas, one terrestrial and the other marine. The fresh water fauna is more closely related to the terrestrial than to the marine and interchange is not particularly common, there being no typical brackish water fauna. Following the suggestion of Simroth (1891) he concluded that terrestrial nemas are more primitive than marine. This view also presumes that other early forms of life (i. e., Bacteria, Algae, Rotatorians, etc.) were originally terrestrial or fresh water and subsequently marine.

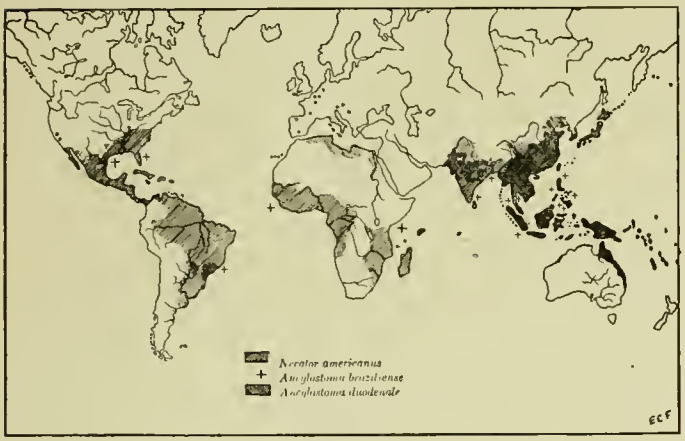

Fig. 143.

Geographic distribution of *Necator americanus* and *Ancylostoma duodenale*. From Craig & Faust, Clinical Parasitology, Lea & Febiger.

HOST GROUPS. Plant parasitic nemas are usually so non-specific as to host that the information derived therefrom is of questionable significance. Animal parasites present much more usable information. Thus we note that the Strongylina make their first appearance in amphibians and reptiles and are found in birds and mammals but not in fish. All strongylins of marine mammals belong to the Metastrongyloidea. Furthermore the Strongyloidea and Trichostrongyloidea (both without intermediate hosts) are parasites of all groups above fish while the Metastrongyloidea are confined to birds and mammals. On that basis one would say that without doubt the Strongylina originated with the amphibians or reptiles and that the adaptation to intermediate hosts was secondary. We would presume the Strongylina to have arisen with the Amphibia and probably from a rhabditoid with two subventral excretory glands similar to those of *Rhabditis strongyloides*.

In the Ascaridina, the Oxyuroidea include parasites of insects, millepeds, amphibians, reptiles and mammals with a few aberrant species (*Rondonia rondoni*, *Monhysterides piscicola*) inhabiting fresh water fish. These latter infections seem to have occurred secondarily. The Oxyuroidea seem to have originated with the millepeds, scarabeids and cockroaches. It is particularly interesting to note apparently identical species of nemic parasites in millepeds from Australia and from the United States. In the Ascaridoidea, which occur in land molluscs, fish, amphibia, reptiles, birds, and mammals, one comes again to the problem of intermediate host. All nemic parasites of fish and marine mammals have intermediate hosts but intermediate hosts occur in the development of ascaridoids parasitic in all other vertebrate groups. The intermediate host is known to occur only in one subfamily of the Ascaridoidea, the Anisakinae. The family Cosmocercidae which is morphologically the simplest (i. e., most rhabditoid) includes species that occur in amphibians and reptiles, with occasional aberrant forms in snails. The Kathlaniidae are more typically parasitic in reptiles, while the Heterakidae are reptile, bird and mammal parasites. Excluding morphologic considerations, one might argue that the Anisakinae (Ascarididae) are the most primitive since they occur in fish. However, secondary entrance of Anisakinae into fish which came up rivers to feed would be ample explanation of their parasitism. Absence of any aquatic (marine) nema with lateral excretory canals makes fresh water or more typically land origin mandatory. We presume the Ascaridoidea arose from the Oxyuroidea, hence from insect parasites. These, in turn, probably originated from a rhabditoid with an H-shaped excretory system similar to that of *Rhabditis dolichura*.

The origin of the Spirurida is indeed dubious and possibly lost in antiquity. No adult forms are found in insects, millepeds or other invertebrates. The Camallanoidea are characteristically parasites of fish and

Fig. 144.

Geographic distribution of *Wuchereria bancrofti* and *Dipetalonema perstans* (*Acanthocheilonema p.*). From Craig & Faust, Clinical Parasitology, Lea & Febiger.

reptiles while the Dracunculoidea and Spiruroidea are parasites of fish, amphibians, reptiles, birds and mammals, and the Filarioidea are parasites of all vertebrate groups except fish. The latter (fish) are the lowest normal final host of the Spirurida. Since all members of the order require an intermediate host, it might be logical to assume an aquatic origin for the group. However, there is no reason for assuming the intermediate host antedates the final host, but quite the reverse, closely related species may have extremely diverse intermediate hosts according to the opportunities and habits of the final host. If we were to suggest any group as being similar to possible ancestors of the Spirurida, it would be the Cylindrogasteridae (Rhabditoidea).

Dioctophymatoids all have intermediate hosts; examples are known that parasitize only birds and mammals in the adult stage while fish, amphibians, and reptiles may act as secondary intermediate hosts. Evidently the Dioctophymatoidea are primarily aquatic forms which arose after the origin of birds and mammals—hence an extremely recent group. All groups of vertebrates harbor trichuroids. Those that occur in aquatic animals have intermediate hosts but species of *Capillaria* from terrestrial mammals differ from one another in this respect. One might suspect the Trichuroidea as being as old as the Vertebrata but in that case one would need to assume that the direct-life-cycle Trichurinae (parasites of mammals) developed from the partially indirect-life-cycle Capillariinae. As in the Dioctophymatoidea, one would trace them back to an aquatic nematode. There is no clear evidence as to whether this nemic group was marine or fresh water but from the fact that speciation continues in land animals while marine species are relatively less numerous, one could easily conceive a fresh-water origin. *Cystoopsis*, a parasite of fish, is probably the most primitive genus. The Mermithoidea are parasitic mainly in fresh water and terrestrial arthropods (Tracheata) but do occur in Crustacea. Steiner (1917) derived the Mermithoidea from the Dorylaimoidea while Fülleborn (1923) gave the same origin for the Trichuroidea. Evidence from comparative anatomy in-

dicates the Trichuroidea developed from forms very similar to present day mermithoids.

Baylis (1938) supplies a further discussion of the host distribution of nemas.

EMBRYOLOGY. In all of the nematodes thus far investigated the embryology may be considered identical for comparative purposes. Bilateral determinate cleavage must certainly have been a characteristic of the nemic ancestor; the resultant adult must have been composed of few large cells, probably about 600, exclusive of the reproductive system. Only one to two eggs were produced at a time. Furthermore, a very close phylogenetic relationship should be supported by similar tissue origins from the primary somatic stem cells arising at the first five cleavages (see Section II Chapter II).

ONTOGENY. The primitivity of meromyarian nemas has been concluded (p. 219) on the basis of embryonic development as well as comparative anatomy. Oligocyty in the intestinal epithelium (p. 101) and cylindricity of the stoma (p. 231) seem also to have been characters of the primitive nema.

COMPARATIVE ANATOMY. The primitive nema will be described, in so far as present evidence permits. Universal attributes of nemas must be included. While they do not limit the ancestor, they define potentialities which must have existed at the origin of the group. Among the universal attributes are a layered, protein cuticle formed as a deposit (differentiated) by the hypodermis, longitudinal somatic muscles, a pseudocoelome, a triradiate esophagus, and a tubular intestine composed of one cell layer. In addition, it seems clear that the hypodermis (p. 34) must have been composed of a few large cells, the cell bodies grouped in four longitudinal chords, modifications therefrom (*Trichuris*) being secondary. The somatic musculature is presumed to have been meromyarian (p. 40). Transverse somatic muscles and specialized muscles (p. 42) might conceivably be remnants of a more widespread system of muscles; hence a double system of musculature is not out of the question. Whether or not the coelomocytes should be interpreted as a system on the wane (reduced parenchyma) or more ancient but homologous to the parenchyma system of the Platyhelmintha is not clear. We tend to accept the latter view. The esophagus and esophagointestinal valve may be considered primary invagination (stomodeum) while the stoma is secondary invagination (hence more comparable to the ciliated "Schlundrohr" of rotatorians). Cuticular lining of esophageal and rectal structures must be presupposed in the primitive nema. As to the intestine, a few large cells lined by a bacillary layer (possibly reduced cilia) seems obvious. Rectal glands are by no means universal but their existence in the majority of phasmidian groups and at least in some aphasmidians (*Anaplectus granulosus*) indicates a primary existence.

As to the nervous system, much can be said, but little proved. Apparently all nemas have paired amphids connected indirectly (through a commissure) with the nerve ring; these amphids consist of a terminal pocket into which sensory terminals and a gland empty. Postembryonic development (p. 229) indicates that they were postlabial in position. Circumoral tactile papillae are also universal and they connect directly with the nerve ring. Serial sublateral tactile organs are, for the most part, confined to one subclass, the Aphasmidia, but might well be primitive. Specialized lateral tactile organs (deirids) are confined to the other subclass (Phasmidia). Posterior lateral organs, phasmids, similar in structure to the amphids are also confined to the Phasmidia but might well be primitive. Male tactile organs are practically universal but whether the paired system of the Phasmidia or the unpaired system of the Aphasmidia is primitive we cannot say. The fundamental architecture of the central nervous system is so set that it leaves little room for question. An anterior commissure, the nerve ring, connects the dorsal, subdorsal, lateral and subventral cephalic ganglia with each other and with the chief nerve which is a more or less double system of incompletely separated ganglia. The nerve ring is not as completely closed ventrally as dorsally indicating that closure may have occurred recently. From the nerve ring six anterior cephalic nerves and a lateroventral commissure connect with anterior sensory organs, while eight direct innervation processes connect with anterior muscles and six posterior motor nerves (the mediodorsal and subventral as well as the laterodorsal and lateroventral somatic nerves function as motor nerves). One or two lateral sensory nerves are also connected with the nerve ring. The ventral or subventral nerves are the chief nerves of the body and connect through commissures with the reproductive system, rectum, copulatory organs and other nerves.

The excretory system (p. 125) has been considered as of double ontogenetic origin. One could interpret the one-cell aphasmidian system as most primitive but it would not account for the tubular phasmidian system. The terminal duct cell of the H-shaped system is apparently the homologue of the aphasmidian system and, if so, the H-shaped system should be considered primitive.

The reproductive system is a very real stumbling block. Seurat's concept of simplicity (p. 191) is easily accepted but ontogeny and comparative anatomy of free-living nemas entirely oppose both Steiner's and Seurat's ideas concerning parallel paired gonads opening posteriorly in both sexes. Even in the male, we must for the time being presume opposed gonads as primitive, at least at the time nemas originated.

Sublateral hypodermal glands and caudal glands must be considered possible attributes of the nemic ancestor. In conclusion, we will reemphasize the point that from each organ system studied, we concluded that the primitive nema must have been a composite of plectoid and rhabditoid characters and only that with such an organism could the later progeny be explained. If this is true, we might expect a saprozoic life in moist soil or swampy habitat.

Relationships with Other Groups*

The above requirements with respect to cuticle (in some representatives at least), esophagus and intestine are met with in the Rotatoria, Gastrotricha, Echinodera and Tardigrada. In all of these groups, except the Echinodera, the pharynx (i. e., muscular foregut) is triradiate, a term which would be applicable to the nemic esophagus; the esophagus in these forms corresponds to the esophago-intestinal valve in nemas. The musculature and body cavity conform in the first three groups. There is as yet no parallel to, or explanation of, the innervation process of the nemic muscle cell which seeks the nerve rather than vice versa. This apparent contradiction may not be as basic as it seems superficially (see p. 172). The nervous system presents some contrasting points. If we assume a "gravitational hypothesis" the nemic nervous system might be rationalized. The ventral nerve is partly paired and the amphidial nerve connection would be direct were the subventral nerves separate and rather lateral in position. If the bulk of the cephalic ganglia were similarly shifted dorsad, the nemic nervous system would correspond remarkably not only with that of the above mentioned groups but also with that of the Platyhelmintha. Even in rotatorians, which are usually characterized as having a "dorsal" nervous system, the two subventral nerves are the chief nerves of the body and the anterior ganglia (brain) are often lobed so that they are lateral as well as dorsal. A cylindroid body form and vibratile to serpentine locomotion could have caused the ventral gravitation of the system. The acanthocephalan and nematomorphan systems could be rationalized with the Rotatoria-Platyhelmintha system in the same manner. There is no especial similarity of either with that of the nematode. We would rather assume convergence. This gravitational view is the one adopted by annelid and arthropod morphologists (see Snodgrass, 1935) for the formation of paired ventral nerves in those groups. It also helps to explain the unpaired ventral nerve of echinoderids (Fig. 145) which are otherwise so much like gastrotrichs.

The excretory systems of rotatorians, gastrotrichs, echinoderids, acanthocephalans and platyhelminths are

*In the following pages the Pearse (1936) system of uniform endings is followed. With minor exceptions, the comparative anatomy as herein presented supports the Pearse Classification. The inclusion of the Class Nemertea within the phylum Platyhelmintha is not supported. It is here placed as a phylum in the series Parenchymata. The phylum Nemata (Cobb, 1919) Pearse, 1936 is substantiated.

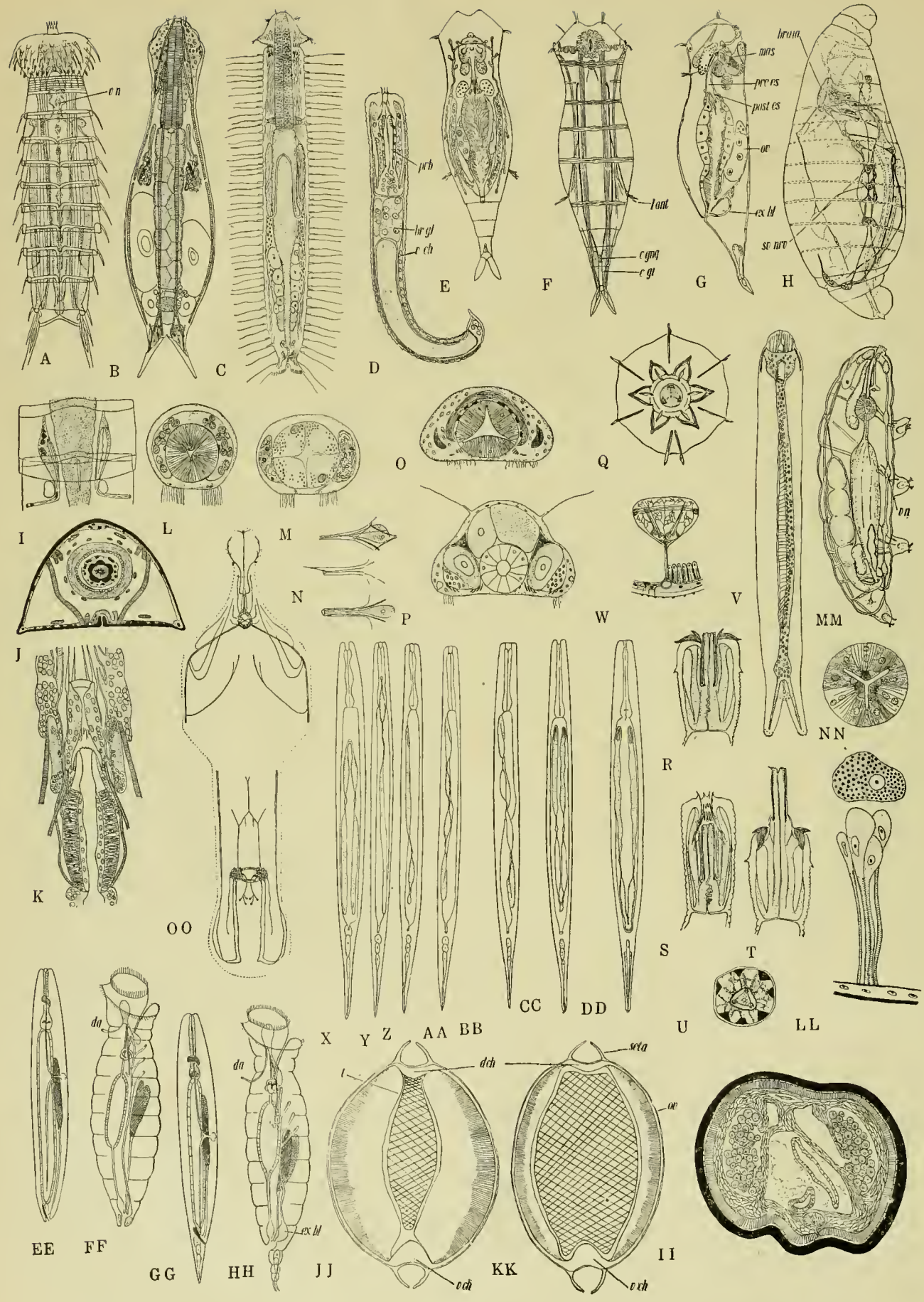
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Fig. 145.

all true protonephridial types including terminal flame cells. In all these groups the system opens posteriorly through either a single orifice, paired separate orifices, or in a cloaca. The nemic tubular system presents a very striking resemblance to the protonephridial system but despite conscientious efforts terminal flame cells have not been demonstrated. The canalicular H-shaped system could be homologized (barring flame cells) with the rotatorian system if we conceive of a new terminal duct connecting with the anterior junction (Huxley's anastomosis) of the lateral canals of Monogonontea rotatorians (see Remane, 1929). The auxiliary excretory system of certain female rhabditids has a striking superficial resemblance to the paired system of gastrotrichs.

The amphids of nemas seem to check well with the retrocerebral organs of rotatorians and the lateral organs of gastrotrichs, rhabdocoele turbellarians and trematode larvae. Paired lateral or sublateral glands or glandular setae have their counterparts in the adhesive gland tubes of gastrotrichs, the deirids (cervical papillae) have been compared with the lateral antennae of rotatorians, while the phasmids may be compared with the caudal antennae (Kaudaltaster) of monogonontic rotatorians, and the caudal glands and spinerette with the paired caudal toes of both rotatorians and gastrotrichs. The existence of three caudal glands and a single spinerette is not especially objectionable in such a comparison since each of the two toes of gastrotrichs may be provided with three such glands.

The somatic musculature, triradiate esophagus, cuticle, and lack of parenchyma all seem to argue for closest relationship of nemas with the rotatorian series. The non-symmetric pharynx of platyhelminths (Turbellarea and Trematodea) while undoubtedly homologous to the triradiate pharynx (nemic esophagus) of the rotatorian series, must be considered as indicative of a separate phylogenetic branch. The reproductive system gives no help nor does it indicate any other possible relationship. In the Gastrotricha we do find separate openings in both systems (hermaphrodites); usually they are posterior but occasionally they are anterior and the gonads are always parallel. The opposed gonads must have been coincident with elongation (hence origin) of nemas and dependent on the essential nemic body form.

Throughout this publication we have tended to question total absence of cilia in nemas (so-called arthropod character*), there being so many suspicious cases where a ciliate structure seems clearly present but vibration has not been observed. Contrast with arthropod and annelid characteristics (lack of true metamerism and of a true coelome, musculature, lack of arthropod chitin in the adult exoskeleton, different symmetry etc.) seems so obvious we feel no need for special discussion. One point, the rectal glands of nemas and their comparison with malpighian tubules, warrants thought, especially when one considers multiplication of these glands (p. 115) and the resultant similarity to those of tardigrades. If there were anything to this we would have to hypothesize arthropods as derived from primitive nemas via the Tardigrada, which view would be objectionable to all good entomologists. It is probably a matter of convergence. Oddly enough, the only other counterpart for the rectal glands is in the anal glands of gastrotrichs.

Determinate bilateral rather than radial cleavage sets the Rotatoria, Gastrotricha, Echinodera, Nemata and, according to some authors, the Acanthocephala (Nematomorpha not investigated) apart from platyhelminths, annelids, and arthropods. Absence of nurse cells in the egg, triradiate esophagus (when present) and external cuticle provide further differentiating characters separating the first five groups from the Platyhelmintha. Musculature does not provide a clear basis of separation, nor does parenchyma (see *Gordius* vs. *Nectonema* within Nematomorpha). However, pending further evidence we will conclude this discussion by accepting the Aschelmintha concept (Rotatoria-Gastrotricha-Echinodera-Nemata-Acanthocephala-Nematomorpha)† and placing it in a superior group Protonephridia which would also include the Platyhelmintha (Turbellarea-Trematodea-Cestodea) and the Nemerta.

Tabular Comparison of Groups

Purely for supplementary consideration a table is given in which there are brief characterizations of the various organs of some of the invertebrates (Table 4). The writer has used this table in teaching and found it of some value. A conscientious attempt was made to attain accuracy but doubtless there are many errors.

Based on the anatomical characters given in table 4, a system was devised whereby the degree of similarity of each group with every other group could be expressed numerically. Each anatomical category was assigned a value of 6. Thus in table 5 the Trematodea are compared with the other groups in respect to each of the 16 anatomical characters given in table 4. Recorded in column 1 of table 5 are scores based on a comparison of the exoskeleton. When the exoskeleton of the Trematodea was compared with that of the Nemata a score of 0 was given, indicating no similarity; when compared to the Rotatoria a score of 4 was given, indicating a certain degree of similarity, etc. In the next vertical column (2) scores are recorded based on the ectodermal epithelium, in the third vertical column (3) scores based on the somatic musculature, etc. The scores are totaled in the right hand vertical column. In this table, it will be noted, the Trematodea are compared *with the Trematodea*, resulting in a total score of 96 which is, of course, the highest possible score. In the following discussion the score of a given group when compared with itself will be referred to as the *base score*.

A similar table was prepared for each of the 12 other invertebrate groups under consideration. These tables are not reproduced herein but the totals, i. e., the scores in the right hand vertical column of each are assembled in table 6. Thus in vertical column "N" of table 6 are recorded the scores resulting from a comparison of the Nemata with the other groups. In the following discussion these scores will be referred to as the *Nemata score series*, those in the next vertical column as the *Rotatorian score series*, etc. When information regarding one or more anatomical feature was lacking the base score is less than 96, as for example, the base score for the Echinodera, Rotatoria and Acanthocephala is, in each case, 90, and for the Gastrotricha, 84.

Whether or not this system is valid, it gives an interesting numerical comparison of apparent similarities. By using all organs the stress of possible convergent characters is lowered. We regard the relative as well as the actual scores as having significance. In each

*Dr. H. J. Van Cleave states Foster reported cilia from the gonoducts of crabs.

†In the following discussion (Tabular comparison of gronps) it will be seen that an evaluation of morphological similarities removes the Acanthocephala to the Platyhelmintha.

Fig. 145. RELATIVES OF NEMATODES

A—Cyclorhagae (Echinodera), ventral view. B—*Chaetonotus* (Gastrotricha), ventral view. C—*Turbanella cornuta* (Gastrotricha), ventral view. D—*Gordius aquaticus* (Nematomorpha), lateral view of larva. E-G — Monogononta (Rotatoria) (E — Dorsal view; F — Ventral view; G — Lateral view). H — *Zelinkiella synaptae* (Rotatoria), nervous system. I-K—*Pycnophcs communis* (Echinodera) (I—Excretory system; J—Cross section in pharyngeal region; K—Horizontal section of pharyngeal region). L-M—*Chaetonotus maximus* (Cross sections, L—At level of pharynx; M—At level of intestine). M—*Macrodasys* (Gastrotricha) (Adhesive tube setae of various types). O-P—*Turbanella cornuta* (Cross section, O—At level of pharynx; P—At level of intestine). Q-T—*Gordius aquaticus* larva (Q—En face view; R-T—Proboscis region in various stages of contraction). U—*Gordius* larva (Cross section near base of proboscis). V-W—*Gordius* adult (V—Cross section of ventral chord showing ganglion cell groups; W—Diagram of nervous system). X-DD—Diagrams of female reproductive system of nemas (DD—Hypothetical form). EE-HH—Comparison of nemas and rotifers (EE-FF—without caudal glands; GG-HH—with caudal glands). II—*Gordius tolosanus* (Cross section of female) JJ-LL—*Nectonema agile* (Nematomorpha) (JJ—Cross section of male; KK—Cross section of female LL—Muscles and oocyte). MM-NN—*Macrobiotus hufelandi* (Tardigrada) (MM—Female; NN—Cross section of pharynx). OO—Diagram of nervous system in Acanthocephala. A & I-K, after Remane, 1928, Die Tierwelt der Nord-u. Ostsee, Part 7d 2; B & L-P after Remane 1929, Handb. Zool. v. 2 (6); D & Q-T after Dorier, 1930, Recherches biologiques et systematiques sur les Gordiaces. Thesis Grenoble; E-G, after Remane, 1929, Die Tierwelt der Nord-u. Ostsee part 7 e; U, after Schepotieff, 1908, Ztschr. Wiss. Zool. v. 89; V-W & OO, after Brandes, 1899, Abhandl. Naturf. Gesellsch. Halle, v. 21; X-DD, After Steiner, 1919, Untersuchungen ueber den allgemeinen Bauplan des Nematodenkoerpers, Jena; EE-HH after Steiner 1919, Festschrift f. Zschokke (31); II, after Ranther 1905, Jena Ztschr. v. 40, n. f. v. 33 (1); JJ-LL after Feyel, 1936, Arch. Anat. Microsc. v. 32; MM-NN after Cuenot, 1932. Faune de France (24).

Table 4. Comparison of nemas with other animals. (Cont. p. 199).

Group	Exoskeleton	Ectodermal Epithelium	Somatic Musculature	Metamerism	Body cavity
Nemata	Cuticle (protein); striated or rarely annulated	Chords-hypodermis	Longitudinal layer attached; transverse few attached ends.	Pseudometamermism in transverse musculature; sometimes in mesenterial cells; sometimes in external annulation and seta distribution also in ganglia.	Pseudocoelome containing fluid and fixed coelomocytes; mesenteries present.
Rotatoria	Cuticle, cilia at head, some external annulation	Hypodermis not differentiated	Longitudinal and transverse (circular) attached only at ends. No complete layer	Pseudometamerism of transverse muscles and ganglia in some	Pseudocoelome containing fluid and amebocytes, filaments present.
Gastrotricha	Cuticle sometimes entire surface ciliated	Hypodermis not differentiated	Longitudinal attached at ends; No complete layer.	None except paired setae	Pseudocoelome containing fluid and free amebocytes
Echinodera	Cuticle annulated	Hypodermis not differentiated	Longitudinal and transverse both attached at ends; No complete layer	Pseudometamerism of exoskeleton; transverse musculature and ventral ganglia	Blastocoele containing fluid and mesenchymatous conn. tissue
Acanthocephala	Cuticle striated	Hypodermis pseudostratified columnar	Longitudinal internal and circular external in 2 layers attached throughout	Pseudometamerism in some	Pseudocoelome containing free cells
Nematomorpha	Cuticle	Pseudostratified columnar ventral chord	Longitudinal attached throughout layer	Serial pouches of gonads; Pseudometamerism of larva	Pseudocoelome usually containing fixed parenchyma cells in fluid
Tardigrada	Cuticle some annulation	Squamous.	Attached at ends 1 muscle 1 cell longitudinal and transverse	Probably true; 4 pairs ventral ganglia and 4 pairs legs	Coelome formed by 4 pairs of evaginations of intestine
Arthropoda	Chitin, annulated	Squamous to columnar	Attached at ends; striated	True paired jointed appendages; metameric ganglia	Coelome filled with fluid
Annelida	Cuticle annulated	Chords and columnar	External circular; internal longitudinal; 2 layers	True internal metameric ganglia	Coelome filled with fluid
Turbellarea	Epidermis often ciliated	Pseudostratified columnar	Circular and longitudinal layers	None	Parenchymatous
Trematodea	Do.	Do.	Do.	Do.	Do.
Cestodea	Do.	Do.	Do.	Reduplicate in Cestoda, not in Cestodaria	Do.
Nemertea	Do.	Do.	Ext. circular; int. longitudinal; int. circular; int. longitudinal layers	Pseudometamerism of gonads and gut pockets	Rhynchocoelome and parenchyma

Table 4. (Continued).

	Stomodeum	Mesenteron	Proctodeum	Excretory system	Nervous system
Nemata	"Esophagus" triradiate, stoma 2nd invagination	Cuboidal 2 cell-rows to columnar epithelium bacillary layer simple	Cuticularly lined rectal glands often, ventral anus	Lateral canals joined anteriorly; ventral secondary orifice; no flame cells	Partially fused vent. nrv. indistinct series of ganglia; nrv. ring with large lateral & ventral cephalic ganglia
Rotatoria	Triradiate "mastax" grossly bilateral	Columnar or cuboidal epithelium, cilia. Simple.	Cuticle lined dorsal anus	Lateral canals joined anteriorly, open together posteriorly into cloaca; flame cells	Ventrolateral paired nerves; with serial ganglia dorsal and dorsolateral cephalic ganglia
Gastrotricha	Triradiate "pharynx"	Cuboidal epithelium 4-8 cell-rows up; no lining. Simple.	Cuticularly lined; anal glands sometimes; anus dorsal or ventral	Lateral canals not joined, open separately in midregion on ventral side; flame cells	Dorsal and lateral cephalic ganglia and lateral nerves
Echinodera	Non-radiate	Columnar epithelium, no lining. Simple	Cuticularly lined terminal or ventral	Short lateral canals; not joined; open separately, laterally; flame cells	Dorsal and lateral cephalic ganglia, lateral and unpaired ventral with series of ganglia
Acanthocephala	None	None	Cuticularly lined cloaca;	Lateral canals open together posteriorly; flame cells	Nerve ring† with associated ganglia; lateral somatic nerves. †Questioned by Van Cleave
Nematomorpha	Non-radiate. ? Proboscis of larva might be triradiate	Columnar epithelium. Simple	Cuticularly lined terminal	None	Nerve ring with circum esophageal ganglion mass and ventral ganglion mass with serial nerve branching.
Tardigrada	Triradiate "bulb"	Cuboidal; with bacillary layer. Simple	Cuticularly lined with "Malpighian" tubules. Ventral anus	? Malpighian tubule	Nerve ring with subdorsal and subventral ganglia and paired ventral nerve with 4 pairs of ganglia
Arthropoda	Non-radiate or superficially triradiate pharynx	columnar with bacillary layer; often highly differentiated and with 2 muscle layers	Chitin lining partial, malpighian tubules	Malpighian tubules or head glands	Circumesophageal commissure and paired ventral nerves with metameric ganglia
Annelida	Non-radiate pharynx	columnar with cilia or bacillary layer	Cuticularly lined	Open metameric nephridia	Circumpharyngeal commissure with ganglia, and paired with metameric ganglia
Turbellarea	Non-radiate pharynx	Columnar with cilia or bacillary layer	None or ? atavistic	Lateral canals open separately posterior; flame cells	No ring; subdorsal ganglia; lateral and lateral cephalic subdorsal and subventral somatic nerves
Trematodea	Do.	Do.	Do.	Do.	Do.
Cestodea	None	None	None	Do.	Do.
Nemertea	Non-radiate	Cecum; lateral sacs	Present	Open or closed protonephridia; longitudinal vessels with sublateral orifices	Circum-pharyngeal commissure with dorsal and ventral ganglia and lateral nerves

Table 4. (Concluded).

	Reproductive system	Cleavage	Molts	Respiratory	Circulatory system	Appendages
Nemata	Tubular paired gonads, sexes separate, female ventral separate orifice male ventral cloacal orifice	Bilateral determinate; no regenerate; no true metamorphosis	Present	None	None	Tube glands; posterior spinerette single
Rotatoria	Tubular paired gonads, sexes separate; orifice into cloaca in both sexes	Bilateral determinate; no regeneration; no true metamorphosis	Unknown	None	None	None; posterior paired ahesive toes
Gastrotricha	Tubular paired gonads; hermaphrodites or Orifices separate, ventral.	Unknown	Unknown	None	None	Lateral tube glands; posterior paired adhesive toes
Echinodera	Tubular paired gonads, sexes separate. Orifice paired, paired, lateral or ventrolateral posterior	Unknown	Present	None	None	None, paired caudal adhesive setae
Acanthocephala	Somewhat tubular or ovoid, paired; sexes separate; orifice into cloaca in both sexes	Superficially bilateral, actually radial determinate; metamorphosis	None	None	Lymphatic superficially	None
Nematomorpha	Sac-like paired gonads with linear pockets; sexes separate; open into cloaca in both sexes	? Radial determinate; Metamorphosis	Absent in usual sense. Does shed larval stylets	None	None	None
Tardigrada	Tubular paired gonads; hermaphroditic; orifices of both sexes into cloaca	Radial. No regeneration. No metamorphosis	Present	None	None	4 pairs of legs
Arthropoda	Paired multitubular gonads, sexes separate, female orifice cloacal; male separate or cloacal	Spiral determinate; regenerate; usually metamorphosis	Present	Varied types	Highly developed	Varied jointed appendages
Annelida	Metameric with separate orifices; hermaphroditic	Spiral determinate; regenerate; metamorphosis		None	Highly developed	Metameric gills and setae
Turbellarea	Paired tubular gonads; hermaphroditic; separate orifices ventral	Spiral determinate; regenerate; metamorphosis	None	None	None	None
Trematodea	Do. except gonads saccate	Cleavage? eggs include yolk cells; metamorphosis	None	None	Lymphatic	None
Cestodea	Do.	Do.	None	None	None	None
Nemertea	Saccate, opening directly to outside; bisexual or hermaphroditic	Spiral determinate; regeneration; metamorphosis	None	None	Highly developed	None

TABLE 5.

Trematodea Score Series

	Exoskeleton	Ectodermal epithelium	Somatic musculature	Metamerism	Body cavity	Stomodeum	Mesenteron	Proctodeum	Excretory system	Nervous system	Reproductive system	Cleavage	Molts	Respiratory system	Circulatory system	Appendages	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total
N	0	0	3	2	1	0	5	0	2	2	0	0	0	6	0	0	21
R	4	3	0	3	2	0	5	1	5	5	2	0	X	6	0	0	36
G	3	3	0	5	2	0	5	0	5	5	6	X	X	6	0	0	40
E	0	3	0	2	2	4	5	0	5	3	5	X	0	6	2	0	37
Ac	0	6	6	0	3	0	0	1	5	4	4	1	X	6	6	6	48
No	0	4	3	1	3	4	5	0	0	1	2	1	0	6	2	0	32
Ta	0	3	0	0	0	0	5	0	0	0	2	1	0	6	2	0	19
Ar	0	3	0	0	0	2	2	0	0	0	0	2	0	0	2	0	11
An	0	3	6	0	0	3	2	1	2	0	3	2	X	6	1	0	29
Tu	6	6	6	6	6	6	6	6	6	6	5	4	6	6	2	6	89
Tr	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	96
Ce	6	6	6	5	6	0	0	6	6	6	6	6	6	6	6	6	83
Ne	6	6	4	5	6	6	5	0	5	6	5	2	6	6	0	6	74

Abbreviations: N, Nemata, R, Rotatoria; G, Gastrotricha; E, Echinodera; Ac, Acanthocephala; No, Nematomorpha; Ta, Tardigrada; Ar, Arthropoda; An, Annelida; Tu, Turbellarea; Tr, Trematodea; Ce, Cestodea; Ne, Nemerta.

score series, the groups are arranged in order of score, and breaks in the score series are indicated by transverse lines. It is very similar to the modified grade curve often used in small college classes. Groups necessarily show reciprocal scores but the position in the series is regarded as indicating *degree of similarity.*

The remarkable homogeneity of the Platyhelmintha is emphasized by the minimum score of 80 (with 96 as base score) scoring two groups on the basis of the third group (Turbellarea, Trematodea, Cestodea). In all three instances the position of these groups in the score series is 1, 2, 3. The Nemerta, included as a class in the Platyhelmintha by the Pearse Classification (1936) have fourth high score in two series Turbellarea and Trematodea) with a score of 74, and fifth high score in the third series (Cestoda) with a score of 54. The Nemerta also shows reciprocally close similarity to these groups since in their own score series the Turbellarea, Trematodea, and Cestodea are placed 2, 3, 4. Only in the annelid score series are the Nemerta disassociated from the other three and this may be due to either real or superficial similarity because of circulatory system and body cavity. The Acanthocephala are associated with the Cestodea and Nemerta in five score series. They are placed fourth in the Cestodea series and fifth in the Turbellarea, Trematodea, and Nemerta series. In their own series they place the Cestodea second and Nemerta third. Considering the breaks in the various series, the Series Parenchymata would appear to contain three phyla, namely, Platyhelmintha, Nemerta, and Acanthocephala; the first of these would contain three classes Turbellarea, Trematodea, and Cestodea. Of the latter classes, the Turbellarea show the greatest similarity to the Nemerta while the Cestodea show the greatest similarity to the Acanthocephala.

The Gastrotricha, Echinodera, Rotatoria and Nemata also seem to show reciprocal relationships but not as close as those of the classes of the Platyhelmintha. Thus the Rotatoria (90 base score) provide a basis for scoring Gastrotricha, 64; Echinodera, 63; and Nemata, 57. The Echinodera (90 base score) provides scores of Gastrotricha, 63; Rotatoria, 63; and Nemata, 56. The Gastrotricha (84 base score) provides scores of Rotatoria, 64; Echinodera, 62; Nemata, 45; and Turbellarea, 45. And the Nemata (96 base score with Rotatoria and Echinodera at 6 point disadvantage and Gastrotricha at 12 point disadvantage ††) provides the scores Rotatoria, 57; Echinodera, 56; Tardigrada, 52; and Gastrotricha, 45. The Tardigrada appear in the table as fifth group in the Rotatoria score series, third in the Annelida series, sixth in the Echinodera series and second group in the Arthropoda series (the latter position is reciprocal). It would appear, therefore, that the Tardigrada more correctly belong to the Arthropoda.

The Arthropoda (base score 96) might be said to lay claim to only two close relatives, the Tardigrada and Annelida; the Annelida (base score 90) by the same token, claim distant kinship with the Nemerta with 44 (see discussion above); the Arthropoda, 48; Tardigrada, 44; and Nematomorpha and Acanthocephala, 34. The Tardigrada (base score 96) show similarity to Arthropoda, 61; Nemata, 52; Annelida, 44; Rotatoria, 43; Echinodera, 42; Gastrotricha, 39; Nematomorpha, 34. The Nematomorpha (No) score series (base score 96) provides us with the odd series Nemata and Rotatoria, 42; Acanthocephala and Echinodera, 41; Gastrotricha, 39; Turbellarea, 36; Annelida and Tardigrada, 34; Nemerta and Trematodea, 32; Cestodea, 29; and Arthropoda, 16. This is practically a uniform series with no obvious break.

According to Schepotieff's (1908) illustrations (Fig. 145 U) the proboscis of the larva of *Gordius* is triradiate with one ray directed dorsad instead of ventrad as in nemas. If this is true, the non-radiate symmetry of the adult esophagus may be considered secondary degeneracy due to parasitism such as happens in the development of mermithids (p. 92). The inverted triradiate symmetry also occurs in one group of gastrotrichs. The echinoderid non-radiate esophagus may be interpreted as a modification of the triradiate, which it resembles more closely than that of the turbellarean. May (1919) found that the larval stylets of gordiids and adjoining cuticle are lost at the time the parasite leaves its host; whether or not this should be interpreted as a molt seems ques-

††By disadvantage we mean that due to lack of information there is no statement in one or more brackets in table 4 and the forms are given zero as though the information indicated total dissimilarity, which it does not.

TABLE 6.

Nemi Relationships. Table of Scores.

N	R	G	E	No	No!	Tu	Tr	Ce	Ac	Ne	An	Ta	Ar
N 96	R 90	G 84	E 90	No 96	No 96	Tu 96	Tr 96	Ce 96	Ac 90	Ne 96	An 90	Ta 96	Ar 96
R 57	G 64	R 64	G 63	N 42	N 47	Tr 89	Tu 89	Tr 83	Ce 63	Tu 74	Ar 48	Ar 61	Ta 61
E 56	E 63	E 63	R 63	R 42	E 43	Ce 80	Ce 83	Tu 80	Ne 54	Tr 74	Ta 44	N 52	An 48
Ta 52	N 57	N 45	N 56	Ac 41	R 42	Ne 74	Ne 74	Ac 63	Tr 48	Ce 54	Ne 44	An 44	N 25
G 45	Ta 43	Tu 45	Tu 42	E 41	Ta 39	Ac 45	Ac 48	Ne 54	Tu 45	Ac 52	No 34	R 43	E 23
No 42	Tu 43	Tr 40	Ta 42	G 38	G 39	G 45	G 40	G 39	No 41	An 44	Ac 34	E 42	Ne 23
An 34	No 42	Ce 39	No 41	Tu 36	Ac 36	R 43	E 37	E 30	R 41	No 32	N 34	G 39	No 16
Ac 32	Ac 41	Ta 39	Tr 37	An 34	An 34	E 42	R 36	No 29	An 36	G 32	Tu 32	No 34	Tu 16
Ar 25	Tr 36	No 39	Ac 33	Ta 34	Tu 31	No 36	No 32	R 29	G 33	E 31	Tr 29	Ac 29	Ac 15
Tu 23	Ce 29	Ac 33	Ne 31	Ne 32	Tr 27	An 32	An 29	An 22	E 33	Ar 23	E 25	Tu 21	G 13
Tr 21	An 21	Ne 32	Ce 30	Tr 32	Ne 27	N 23	N 21	N 21	N 32	Ta 19	Ce 22	Tr 19	R 12
Ce 21	Ne 16	An 19	An 25	Ce 29	Ce 24	Ta 21	Ta 19	Ta 19	Ta 29	R 16	R 21	Ce 19	Tr 11
Ne 14	Ar 12	Ar 13	Ar 23	Ar 16	Ar 21	Ar 16	Ar 11	Ar 7	Ar 19	N 14	G 19	Ne 19	Ce 7

tionable. The earlier view that the "praesoma" did not take part in later development was disproved by May. These points all support the inclusion of the Nematomorpha in the Aschelmintha.

If the Nematomorpha were credited unqualifiedly as having molts (No!) then five points more would be scored in comparison with some groups and five deducted from others so that the score series would be Nemata, 47; Echinodera, 43; Rotatoria, 42; Tardigrada, 39; Gastrotricha, 39; Acanthocephala, 36; Annelida, 34; Turbellarea, 31; Trematodea, 27; Nemerta, 27; Cestodea, 24; Arthropoda, 21. In the reciprocal scoring series the Nematomorpha would be included as showing similarities to the Nemata and Echinodera and just under the break of the Rotatoria, Gastrotricha and Annelida series. These indications of similarity support the two diverse schools of thought, the one which is the more popular (and here the more distinct) placing the Nematomorpha in the Aschelmintha or Nemathelminthes, and the other less popular one which relates the Nematomorpha to the Annelida.

On the basis of the information obtained from tables 4 to 6, it appears that there are three groups of the rank series among the organisms considered (Old group Vermes and Arthropoda). These series are as follows: Parenchymata (containing the phyla Nemerta, Acanthocephala, and Platyhelmintha), Aschelmintha, and Annelida-Tardigrada-Arthropoda (Unnamed as far as we know).

The phylum Nemata, proposed by Cobb (1919), apparently constitutes a valid group differing from other groups as much as do the more regularly constituted phyla. It is included within the Series Aschelmintha which also contains the phyla Rotatoria, Gastrotricha, Echinodera and Nematomorpha. The name Nematoda may be retained for a class equivalent in extent to the phylum Nemata or it may be dropped. In the latter instance the subclasses Phasmidia and Aphasmidia would take the rank of classes. In many ways the Phasmidia and Aphasmidia are parallel and might be considered twin classes just as the Gastrotricha and Echinodera are twin phyla. The name Nemathelminthes seems to apply to no natural group.

The position of the Tardigrada within the Annelid-Arthropod series is very clearly substantiated. It is unfortunate that students of the larger segmented forms do not direct some of their attention to the Tardigrada.

A family tree (Fig. 146) sums up the conclusions of the scoring in a graphic manner. No attempt is made to express degrees of primitivity or possible ancestry between one group and another. One could, and the writer has, made scoring tables on the basis of "Degree of primitivity," expressed numerically, but first all variations of all organs need to be rationalized and a description of the primitive condition set forth. This is so subjective that we fear to expose it to public condemnation.

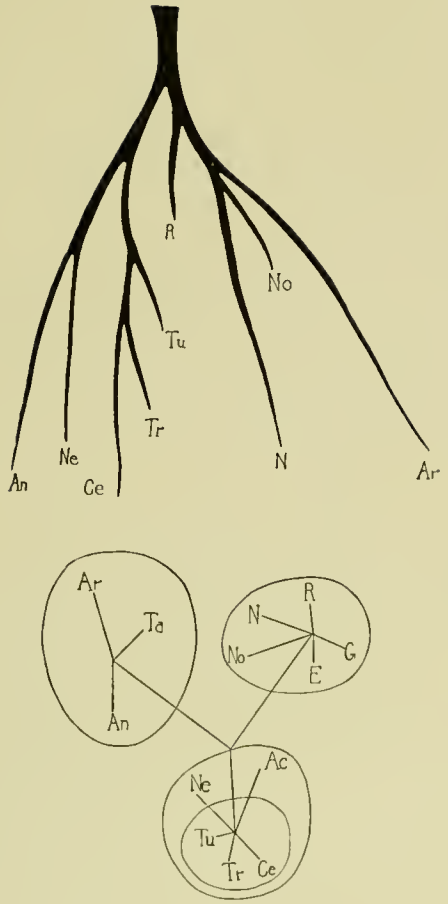

Fig. 146.

Upper figure, Line of Descent, as pictured by Buetschli, 1876, Ztschr. Wiss. Zool. v. 26.

Lower figure, Diagram showing interrelationships as formed on basis of tables 4 to 6.

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ANNOUNCING SECTION II, PARTS II-III
AN INTRODUCTION TO NEMATOLOGY

J. R. Christie, Editor.

Chapter	Title	Authors
IV.	Life History. General Discussion	B. G. Chitwood
V.	Life History. Vagantia and Phytoparasitica	J. R. Christie
VI.	Ecology, symptoms, control and treatment for Vagantia and Phytoparasitica ...	A. L. Taylor, W. L. Courtney, G. Thorne, B. G. Chitwood and J. L. Bassen
VII.	Life History. Zooparasitica	A. C. Chandler, J. E. Alicata, J. T. Lucker, and J. R. Christie
VIII.	Epidemiology and sanitary measures for the control of nemic parasites of domestic animals	T. W. M. Cameron
IX.	Epidemiology and sanitary measures for the control of nemic parasites of man ..	W. W. Cort and E. B. Cram
X.	Treatment of nemic diseases of man and domestic animals	W. H. Wright and P. D. Harwood
XI.	Immunity due to nematodes	Norman R. Stoll
XII.	Feeding habits of nematodes (a) Vagantia and Phytoparasitica	J. R. Christie, G. Thorne, and B. G. Chitwood
	(b) Zooparasitica	J. E. Ackert and J. H. Whitlock
XIII.	Chemical composition and metabolism of nemic parasites of vertebrates ..	Theodor von Brand and Theodore L. Jahn

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